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TIME COURSE AND STIMULUS SPECIFICITY OF INTEROCULAR SUPPRESSION

by

J. BRUCE BALDWIN

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Physiological Optics/School of Optometry, The University of Alabama at Birmingham

BIRMINGHAM, ALABAMA

1996

ABSTRACT

Binocular rivalry (BR) suppression has been shown to selectively suppress the opponent-color system over the luminance system, and to selectively suppress short wavelengths over medium and long wavelengths (Smith, et al., 1982). Flash suppression (FS), a technique designed after Wolfe (1983) by Ooi and Loop (1994) creates "instantaneous" rivalry suppression by suddenly introducing a grating to one eye while viewing a dichoptic, orthogonal grating with the other eye. Unlike BR, Ooi and Loop found that in FS, blue color was suppressed least and the luminance system was suppressed most. Experiment 1 of this dissertation repeated the experiment of Ooi and Loop by measuring suppression of blue (439nm), red (613nm), and luminance (540nm/540nm background) probes presented to the right eye at 50 msec after flashing an orthogonal 2.6 cpd, grating to the left eye. The same probes were also presented at 300 and 500 msec after flashing the left grating. At 500 msec after suppression onset, the FS patterns were similar to those previously reported for BR. Experiment 2 extended the

findings of Experiment 1 with additional subjects and by sampling more times after suppression onset. Blue and red probes show a steady rise time of suppression over the first 500 msec after suppression onset, whereas the luminance probes are suppressed early and show little change over time. In a variation of FS, flash permanent suppression (FPS), the right grating was replaced with a homogeneous field and the time course of suppression determined. In Experiment 3, "color" and "detection" thresholds were compared for 613nm probes during FPS. The results indicate that the luminance and opponent-color systems were each responsible for detection of the red probe at different times after suppression onset. A series of controls for Experiments 1-3 showed "masking" to contribute little to the reduced sensitivity. Permanent suppression (PS) was found to be selective for the duration of colored and luminance probes in Experiment 4. In Experiment 6, suppression of suprathreshold probes was evaluated in a reaction time paradigm. Subjects showed suppression (FPS, FS) to probes with intensities up to 2.5 log units above threshold.

DEDICATION

This dissertation is dedicated to Mary Ann, Matthew, and Scott for all those missed dinners and ball games. Thanks for staying with me all those years and letting me drag you from Birmingham to Phoenix to Roxboro to San Antonio to Birmingham and back to San Antonio.

Furthermore this text is dedicated to mom and dad for rearing me up pretty good in spite of some pretty bad odds.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
BR	Binocular rivalry
cd/m^2	Candela per square meter
cpd	Cycles per degree
FS	Flash suppression
FPS	Flash permanent suppression
log	Logarithmic
LGN	Lateral geniculate nucleus
MAT	Method of adjustment
msec	Milliseconds
nm	Nanometers
ND	Neutral density
PS	Permanent suppression
RT	Reaction time
V1	Visual area 1
V2	Visual area 2
V4	Visual area 4
SEM	Standard error of the mean
2AFC	Two alternative forced choice

INTRODUCTION

Interocular Suppression

Interocular suppression is seen clinically in a variety of abnormal binocular vision conditions, or can be experimentally induced in individuals with normal binocular vision. Clinical suppression is often seen in subjects with strabismus (crossed eye), with or without amblyopia, or in subjects with anisometropic amblyopia (difference in the refractive powers of the two eyes) (Burian and von Noorden, 1974). Animals with strabismus, amblyopia, or both, have an anatomical substrate, in the form of an altered cortical cytoarchitecture, that is responsible for suppression and loss of visual acuity (Hubel and Wiesel, 1965; Crawford, Smith, Harwerth, and von Noorden, 1984). Presumably, humans suffer similar neuroanatomical consequences of visual deprivation (Hitchcock and Hickey, 1980). Early in the visual experience of a young strabismic subject, before brain anatomy is altered, there may be an interocular suppression with a neurophysiological mechanism similar to the suppression that can be experimentally produced in

normal subjects. Suppression of a crossed eye's image may be a response by the visual system to avoid the confusion generated by diplopia. This early suppression response may become permanent only after a certain time period (Hubel and Wiesel, 1970). Knowledge of the characteristics of experimental suppression should help us to understand the process leading to amblyopia and other forms of clinical suppression.

Suppression can be experimentally induced in a variety of ways. Presenting a contoured stimulus to one eye and a contour-free field to the other eye results in a measurable suppression of vision in the eye viewing the contour-free field. This form of interocular suppression is known as "permanent suppression" (PS) (Mauk, Francis, and Fox 1984; Blake and Camisa, 1978) (Figure 1). The more frequently studied condition known as binocular rivalry (BR) results when each eye views separate images that are dissimilar enough to preclude fusion (Figure 1). In lieu of fusion, an alternating suppression of each image occurs. Although there is debate over the nature of the various types of suppression, a more complete understanding of the characteristics of PS and BR will significantly add to our understanding of suppression and help design and test models

Figure 1. Suppression inducing stimuli. A. Binocular Rivalry. Free fusing the gratings and "BR" will result in rivalry when viewed continuously. B. Permanent Suppression. Free fusing the circular fusion locks and "PS" will result in the perception of the left grating. Note: some fading of the grating is evident for prolonged viewing times due to the Troxler effect or to rivalrous spatial detail from the paper on the right side. C. Flash Suppression. FS can be simulated by placing a white card over the left grating and free fusing the "FS." When the card is abruptly removed, the right grating will be suppressed. D. Flash Permanent Suppression. FPS can be simulated by placing a white card over the left grating and free fusing the "FPS." When the card is abruptly removed, the right eye will be suppressed. Note: gratings are not to scale.

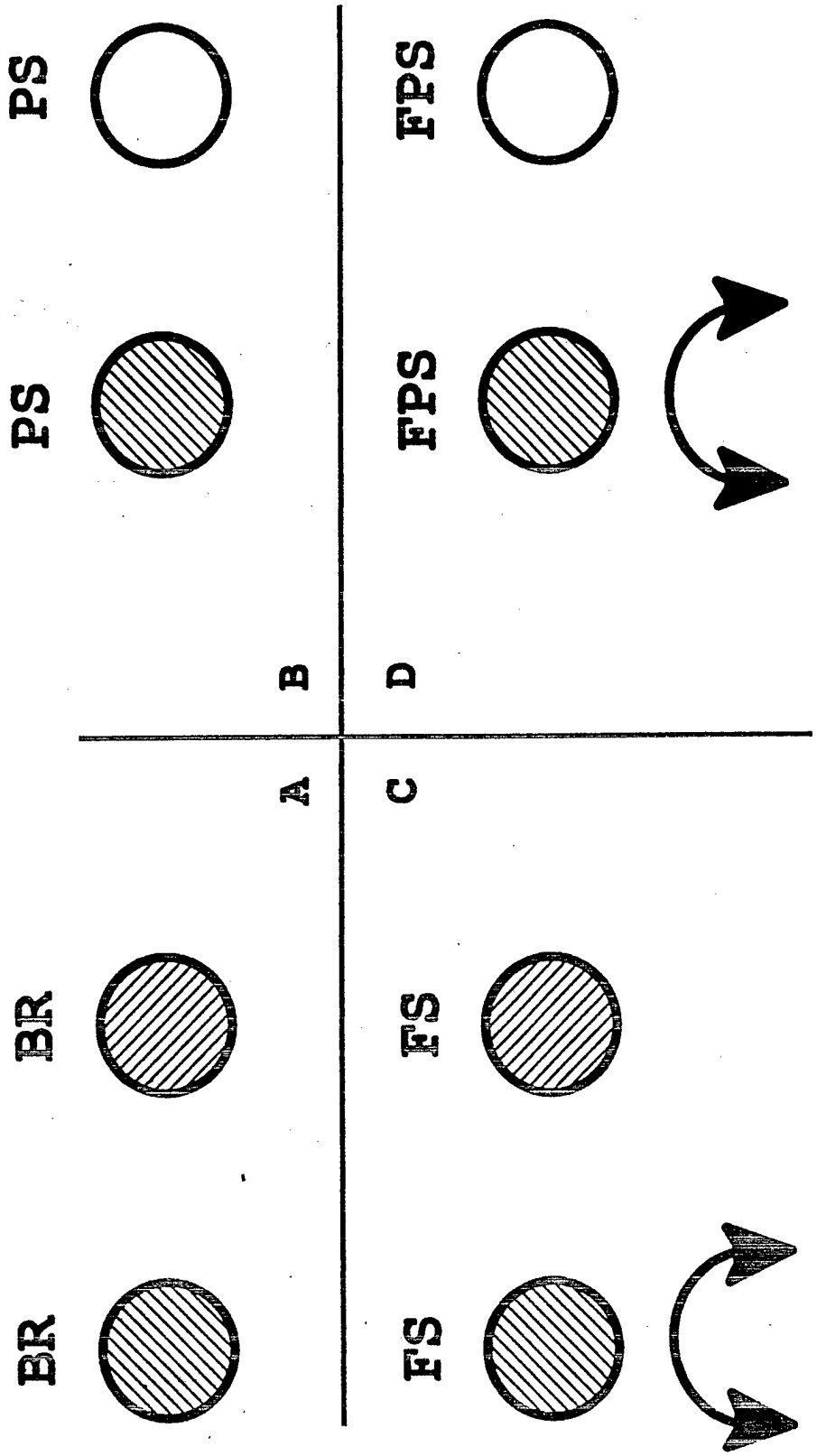


Figure 1.

of the suppression mechanism (Blake, 1989; Lehky, 1988; Wolfe, 1986) and perhaps lead to better treatment for conditions that result in amplyopia. A fresh interest in studies of binocular rivalry has been generated by recent neurophysiological research that seems to identify neurons responsible for suppression. These studies will be considered later.

Binocular rivalry is the most studied form of non-clinical interocular suppression (du Tour, 1760; Breese, 1909; Levelt, 1960; Fox 1991). Traditionally, there have been three main topics of BR studies: 1. Stimulus characteristics are systematically altered, and some function of the phenomenal alternation (dominance or suppression phase) is measured, such as the duration of each suppression phase. In general, increasing the stimulus strength to one eye increases the rate of alternation and increases the total amount of time the stronger stimulus is seen (dominant)(Levelt, 1965). 2. Other studies have investigated the sensitivity of a suppressed eye to changes in stimulus dimensions, such as spatial frequency and orientation (Blake & Fox, 1974), or contrast, (Blake and Camisa, 1979). Changes made by the experimenter to a stimulus that is in a suppression phase of BR usually go

undetected until the suppressed image spontaneously returns to dominance. 3. Still other studies have used a stimulus probe, such as a flash of light (Wales and Fox, 1970) or flashed letters (Fox and Check, 1972) to probe the sensitivity of the visual system during BR suppression. A probe can be presented to an eye while in a suppression phase of BR, and if the intensity of the probe is not too high, the presence of the probe will go undetected.

As reviewed by Fox (1991), most studies of BR have indicated that the visual system non-selectively suppresses information during BR. That is to say that any type of change presented to an eye in a suppression phase goes undetected unless the strength of the stimulus surpasses some criterion level, usually about 0.5 log units above the dominance threshold. This non-selective principal suggests that the visual system is in a static mode with some form of "blockade" to new visual information, most likely at an early level in the visual system such as the LGN or striate cortex (Blake, 1989).

An exception to the principal of non-selectivity was demonstrated by Smith, Levi, Harwerth, and White (1982). They reported that in BR, the opponent-color system is suppressed more than the luminance system (Figure 2). They

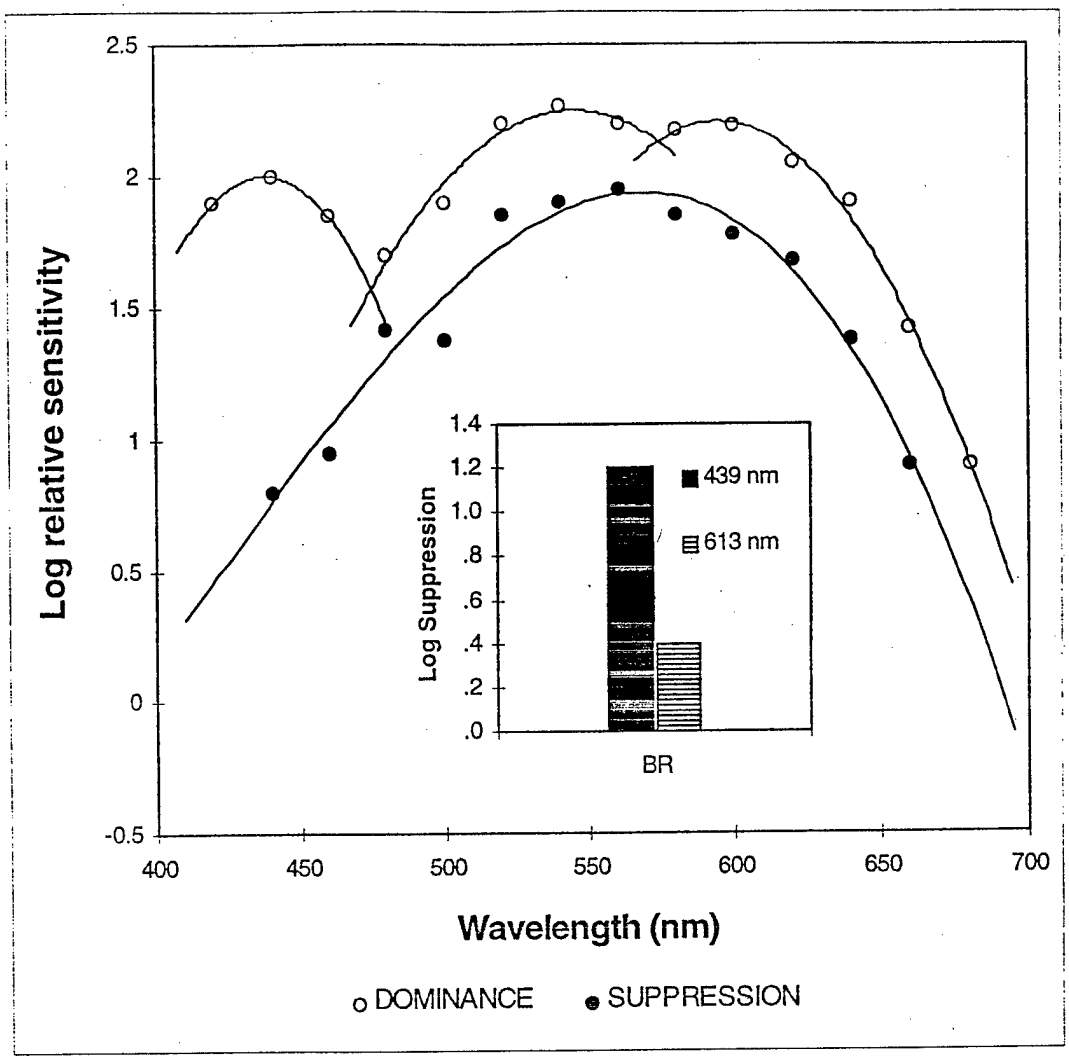


Figure 2. Spectral sensitivity functions during binocular rivalry. Data replotted from Smith et al. (1982). During dominance, the spectral sensitivity function has the three peaked shape characteristic of opponent-color system detection for these 20 msec, .4 x .8 degree probes. During the suppression phase of BR, the subject is less sensitive to the same spectral probes and the shape of the function now looks like the photopic luminosity function. Note that the short wavelength probes are suppression more than others. Inset: graphical display of magnitude of suppression for wavelengths used for stimulus probes in Experiments 1 - 6.

reached this conclusion by observing that the shape of the spectral sensitivity curve during the dominance phase of BR had a three peaked shape, characteristic of the opponent-color system, while the shape during the suppression phase had a single peak and resembled V_λ, the photopic spectral sensitivity function. A stimulus probe, such as a spectral increment used by Smith, et al. (1982), is detected by the visual mechanism most sensitive under the testing conditions (King-Smith and Carden, 1976). During BR suppression, the spectral sensitivity function resembles V_λ, thus the luminance system is most sensitive, which implies that the opponent-color system is suppressed more.

The observations of Smith et al. clearly show selectivity within the mechanism responsible for BR. In addition to selective suppression of the opponent-color system, inspection of figure 2 shows that blue color is suppressed more than other wavelengths. These findings were replicated by Ooi and Loop (1992a,b, 1994). In the course of investigating spectral sensitivity during visual suppression, Ooi and Loop (1994) used a novel procedure to induce rivalry suppression and present a stimulus probe. They had subjects view a high contrast 3 cycle per degree

square wave grating with one eye, and at a time determined by the experimenter, an orthogonal grating was flashed to the other eye for a duration of several seconds. When this orthogonal grating was flashed, the grating viewed by the other eye disappeared from the subject's perception, hence the term "flash suppression." This technique allowed the experimenter to consistently produce rivalry-like suppression without relying on subject reports of suppression in order to determine when a stimulus probe should be presented.

Unlike earlier studies of BR (Smith et al., 1982; Ooi and Loop 1992a,b), during flash suppression (FS), blue color is suppressed less rather than more (Figure 3) (Ooi and Loop, 1994). This finding is important because FS appears to subjects to produce suppression indistinguishable from BR, yet the suppression patterns of spectral increment probes are different.

Ooi and Loop (1994) suggested that the suppression patterns of spectral probes might be different in FS because of the timing of the probe presentation. In BR, a subject must indicate when one eye is suppressed, and a probe is then delivered at some time after onset of suppression. Because of this delay in signaling, in BR, a probe is always

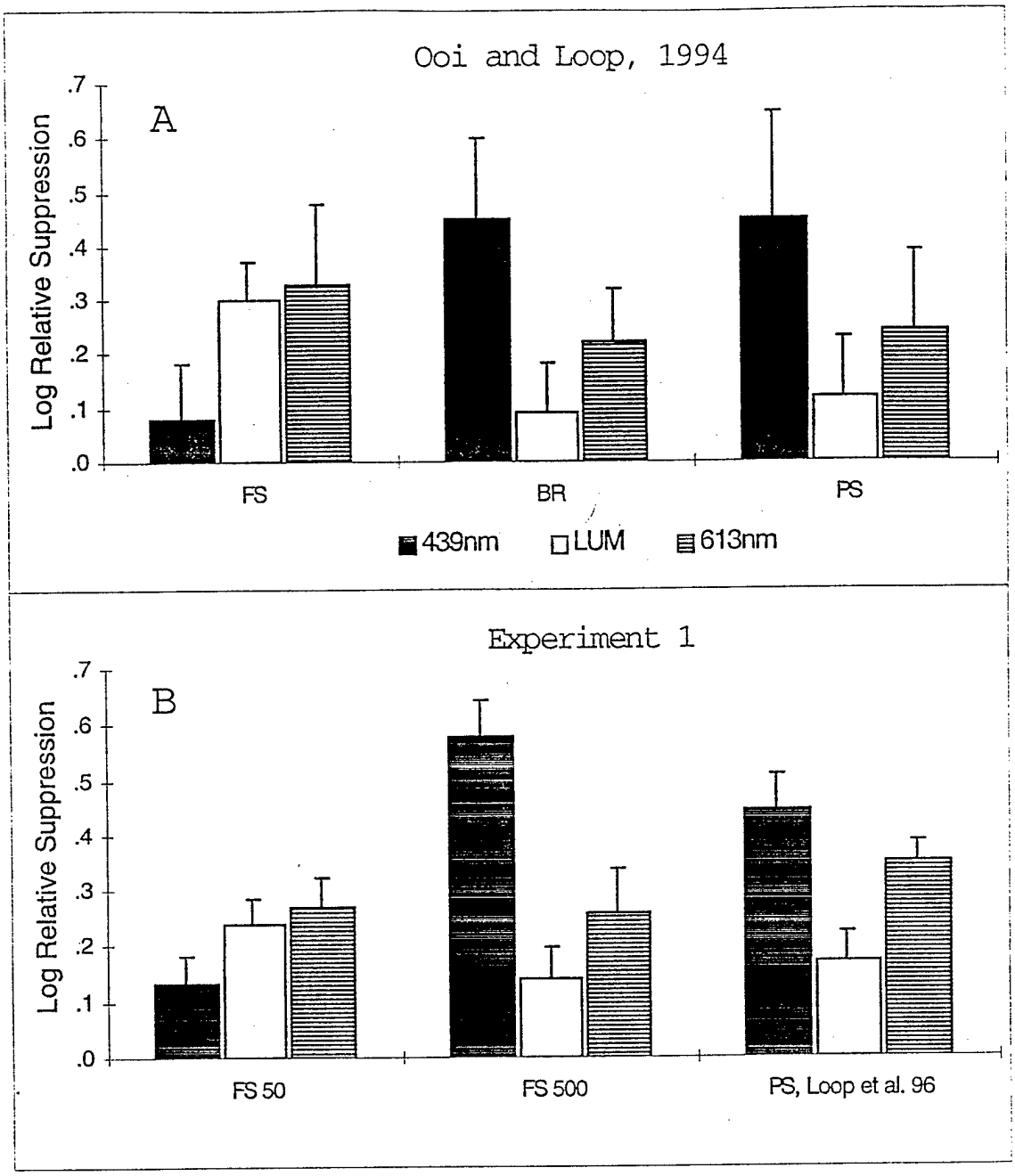


Figure 3. Suppression patterns. A. Suppression patterns for FS (Ooi and Loop, 1994) were different from BR in that blue color was suppressed less in FS and luminance was suppressed less in BR. B. Suppression patterns for FS derived from Experiment 1 and Figure 9. Data on permanent suppression was added for comparison.

delivered at some steady state of suppression on the order of 200 - 600 milliseconds (msec) after onset, whereas in FS, the probe was always presented precisely at 50 msec after presentation of the flashed grating.

The purpose of the investigations presented here centered around investigating the time course of suppression during flash suppression. We have shown that suppression patterns of spectral probes do change over time and are dependent on stimulus characteristics, such as type of inducing stimuli and the size, duration, and wavelength of probes (Baldwin and Loop, 1995; Baldwin, Loop, and Edwards, 1996). The concept and technique of FS is central to the data presented here, and the remainder of the introduction will review the history of FS. Experiments 1 - 5 will present results from investigations of the time course and magnitude of suppression using stimulus probes presented at near threshold intensities. In addition to studies of FS, results will be presented from experiments using a related paradigm we call flash permanent suppression, and permanent suppression. Experiment 6 will explore sensitivities during suppression of suprathreshold probes.

Flash Suppression: Historical Perspective

A commonly used stimulus arrangement for producing BR is a pair of orthogonal square wave gratings as seen in Figure 1. Viewing such gratings dichoptically for an extended period of time results in alternating suppression of each image. The alternation process is not under conscious control (Levelt, 1960) and is stochastic in nature (Fox and Herrmann, 1967) such that the duration of any suppression phase is not dependent on the preceding suppression phases. Viewing dichoptic gratings for extended periods never results in the appearance of a complete crisscross or plaid, except when both gratings are present at near threshold contrasts (Liu, Tyler and Schor, 1992).

Simultaneously flashing two high contrast gratings for short durations, less than 200 msec, can produce a "fused" or plaid appearance. The earliest such report was recorded by Hering (1920/1964) who noted that when dichoptic orthogonal gratings were exposed for only a "fraction of a second," he saw both sets of gratings with equal clarity. Other authors have reported that presenting dichoptic gratings or line targets for short durations can lead to apparent fusion instead of rivalry or suppression of one target (Kaufman, 1963; Goldstein, 1970). It was shown that

short presentation times (less than 100 msec) resulted in a fused plaid while longer presentation times resulted in rivalry (Anderson, Bechtoldt and Dunlap, 1978). Furthermore, Anderson, et al. (1978) also determined that for the longest presentation times (800 msec) subjects only saw rivalry, not fusion followed by rivalry, suggesting that the longer duration rivalry stimulus somehow masked the initial fused appearance seen with short exposure times.

Wolfe (1983) systematically investigated this phenomenon he described as "abnormal fusion." He found that orthogonal dichoptic gratings always appeared fused when viewed simultaneously for less than about 150 msec and that the percept gradually became more rivalry-like with longer durations. One second presentation times always resulted in rivalry for 7 of 9 subjects. He also concluded that this effect was not influenced by the spatial frequency or mean luminance of the gratings; he did not investigate the effect of contrast.

Wolfe (1984) extended these findings by flashing orthogonal gratings to both eyes after one eye had previously viewed one grating. Now, when orthogonal gratings were flashed to both eyes, instead of seeing a fused plaid, subjects always saw only the new grating,

opposite the one previously viewed. Thus the original grating was visually suppressed. This reversal of dominance was only seen if the original grating was viewed for more than 150 msec and the time between viewing the right followed by flashing both gratings was less than 200 msec (Figure 4). These findings suggest that there are competing mechanisms involved in fusion and suppression of "non-fusible" stimuli. Fusion is seen only under certain conditions like short duration simultaneous presentation (Wolfe, 1983) or very low contrast targets (Liu et al., 1992). The term "flash suppression" was first used by Ooi and Loop (1994) although there have been several recent applications of the procedure.

Recent Applications of Flash Suppression

De Bulsunce and Sireteanu (1991) repeated the experiments of Wolf (1993, 1994) and found a similar transition from fusion to BR suppression for simultaneous exposure times greater than 150 msec. In particular, de Belsunce and Sireteanu (1991) and Leonards and Sireteanu (1993) noted that some amblyopic subjects were shown by Wolfe (1986) to have suppression patterns similar to normals (Figure 5). They also compared amblyopic subjects to normals but, unlike Wolfe, found only a few subjects similar

Figure 4. Time course of suppression. Subjects viewed a 3.8 cpd grating with the right eye for one second. The stimulus was turned off, and after some interstimulus interval (ISI), the original right grating and an orthogonal left grating were flashed on simultaneously. Subjects rated the exclusive visibility of the left grating, where "5" is exclusive visibility of the left grating and 1 is binocular rivalry between the two gratings. For ISIs less than 200 msec, the orthogonal left grating completely suppresses the perception of the right grating. Note that the gratings were flashed simultaneously and subjects used an arbitrary rating scale, so actual depth of suppression of the right eye was not determined. Data from Wolfe, J.M. (1984) Reversing ocular dominance and suppression in a single flash. Vision Research, 24, 471-478.

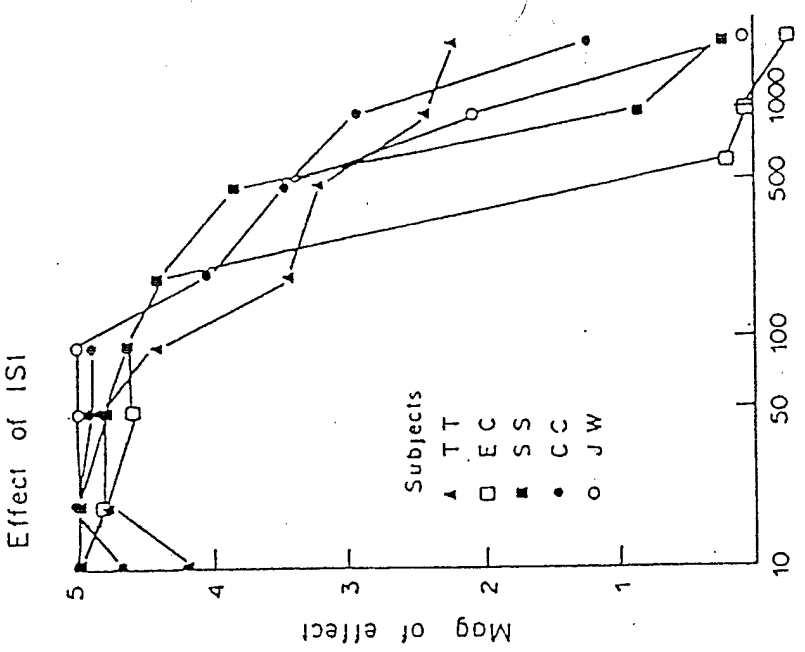

Effect of ISI
Mag of effect
5
4
3
2
1
0
10
50
100
500
1000
ISI (msec)
Subjects
T T
E C
S S
C C
J W

Figure 4.

Figure 5. Time course of suppression, abnormal binocular vision. In a paradigm similar to Wolfe (1983), subjects were simultaneously presented with orthogonal gratings. For short presentation times (<150 msec), normal subjects saw the gratings fused in a plaid like appearance. Longer presentation times resulted in binocular rivalry suppression. Some subjects with abnormal binocular vision had a suppression time course quite different from normals. Data from de Belsunce, S. and Sireteanu, R. (1991) The time course of interocular suppression in normal and amblyopic subjects. Investigative Ophthalmology and Visual Science, 32, 2645-2652.

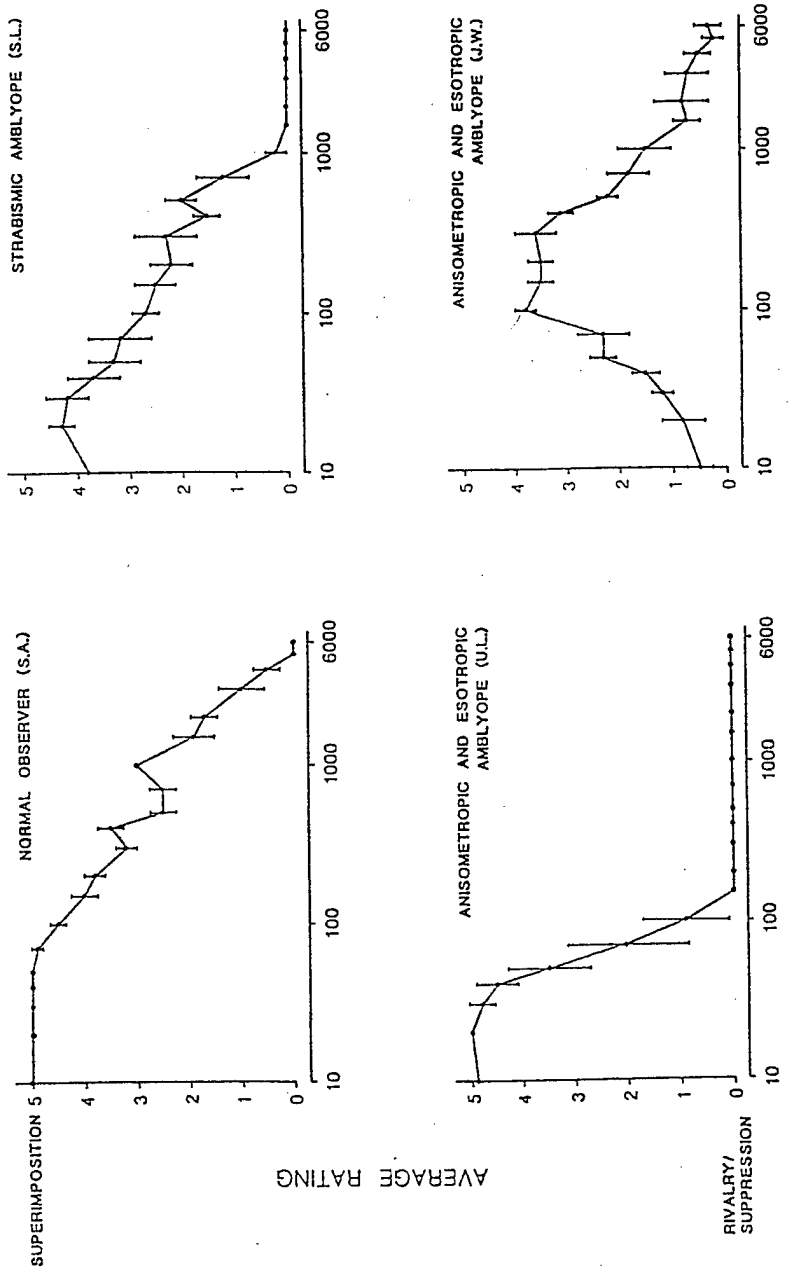

STRABISMIC AMBLYOPE (S.L.)
ANISOMETROPIC AND ESOTROPIC AMBLYOPE (J.W.)
NORMAL OBSERVER (S.A.)
ANISOMETROPIC AND ESOTROPIC AMBLYOPE (U.L.)
SUPERIMPOSITION
RIVALRY/ SUPPRESSION
AVERAGE RATING
STIMULUS DURATION / ms
10
100
1000
6000
0
1
2
3
4
5

Figure 5.

to normals. The other amblyopic subjects had suppression patterns that fell into one of four distinct categories (Leonards and Sireteanu, 1993). Some subjects showed suppression for short duration exposures and others for intermediate or long duration exposures of the orthogonal gratings. These very different suppression patterns could represent different suppression mechanisms for different types of amblyopes, although no correlation was seen in this small sample. When vision in one eye of normals or the better eye of amblyopes was attenuated with neutral density filters, a variety of suppression patterns was produced which led Leonards and Sireteanu to conclude that all subjects "produce suppression patterns belonging to one and the same family of curves." Thus, different suppression mechanisms do not have to be invoked to explain the differences in subjects. A difference in the depth of suppression related to severity of amblyopia may be responsible for the different suppression patterns.

Liu and Schor (1994) used a variation of FS to investigate the spatial extent of the suppression mechanism. There is a limit to the angular extent of suppression produced by crossing lines (Kaufman, 1963). Exploring the extent of suppression is difficult in a large, long duration

rivalry stimulus because instead of a complete appearance of one grating or the other, for targets much over one degree in size, the subject will sometimes see a composite of the left and right gratings (Fox, 1991). Liu and Schor (1994) overcame the problem with composites by having subjects view a single difference of gaussians (DOG) target with one eye and at a predetermined time, flashed an orthogonal double DOG to the other eye. Flash suppression of a defined segment of the single DOG was rated by subjects to determine the spatial extent of the suppression effect. In a similar fashion, Kaufman (1963) had used single and double line targets to measure the extent of rivalry. When he flashed both the single line and the orthogonally arranged double lines simultaneously, he did not get suppression but fusion as noted earlier. His presentation time was always 50 msec and simultaneous, which are both conditions favoring fusion over rivalry or FS (Wolf, 1983, 1984). The limit to the spatial extent of suppression determined by Kaufman (1963) and Liu and Schor (1994) may explain the minimal suppression of tiny probes measured in experiment 4 below.

Probably the most widely reported type of BR experiment involves the measure of dominance and suppression durations (Levelt, 1965, 1966; Fox, 1991). For a given set of

conditions, the dominance and suppression durations are randomly distributed over time, and a subject is unable to consciously force one eye to become or remain dominant. Blake, Westendorf, and Fox (1990) selectively forced dominance of either eye of subjects viewing rivalry targets. A transient increase or decrease in the luminance of one of the rivalry targets was flashed to one eye for 250 msec, and immediately after flashing, subjects always reported a switch to dominance of the flashed eye. Precise timing of this effect was not possible because subjects' report was based on reaction time on the order of hundreds of milliseconds. Blake et al. (1990) determined through an autocorrelation analysis that the distribution of forced dominance durations was sequentially independent, as is the distribution of free running rivalry (Fox and Herrmann, 1967). Furthermore, reversing dominance by this flash suppression technique had no effect on subsequent measures of free running rivalry, although the first dominance and suppression phases were shorter than controls. One can conclude from this experiment that flash suppression allows the experimenter to control the timing of suppression onset without altering the underlying rivalry mechanism.

Baldwin and Loop (1994) measured dominance durations under various stimulus conditions and found that the mean dominance duration was the same for FS and BR under similar conditions. Lowering the background illumination increased the mean dominance duration for both BR and FS as would be expected (Levelt, 1966). Furthermore, we measured dominance durations during BR and FS and plotted the distribution of each. A theoretical gamma distribution was fit to the empirical data (Figure 6). A gamma distribution describes a function where the measures, such as dominance durations, are sequentially independent random variables. The gamma distribution has been used by a number of authors as a "signature" for binocular rivalry (Levelt, 1965; Fox and Herrmann, 1967; Leopold, Sheinberg, and Logothetis, 1996). By inspection, the theoretical curve fits our empirical data quite well considering the small sample size. Statistical analysis (Statistica, v 5.0) indicates that both FS and BR distributions can be reasonably well fit with the gamma function.

BR Kolmogorov-Smirnov: d=.032, p=n.s.
Chi-Square: 4.94, p=.84

FS Kolmogorov-Smirnov: d=.064, p=n.s.
Chi-Square: 9.25, p=.16

Figure 6. Dominance durations. Dominance durations were measured for subject BB during FS and BR. Durations were collected from earlier experiments (Baldwin and Loop, 1994) and an additional experiment using two Tektronix 608 monitors to generate orthogonal gratings. Only left eye dominance durations were measured for both FS (n = 309) and BR (n = 277). The durations were standardized by dividing each duration by the mean of the sample from each experiment. The resulting distribution has a mean of 1.0 and a standard deviation proportional to the original experimental data. A theoretical gamma distribution (Fox and Herrmann, 1967; Fox, Todd, and Bettinger, 1975) was fit to the data with the following function:

$$f(x) = \frac{\lambda^r}{(r-1)!}\left(x^{r-1}\right)\left(e^{-\lambda x}\right) \text{ where } r = \frac{MEAN^2}{VARIANCE} \text{ and } \lambda = \frac{r}{MEAN}$$

The gamma function is considered to be a "signature" for BR and fits the empirical data well considering the small sample size.

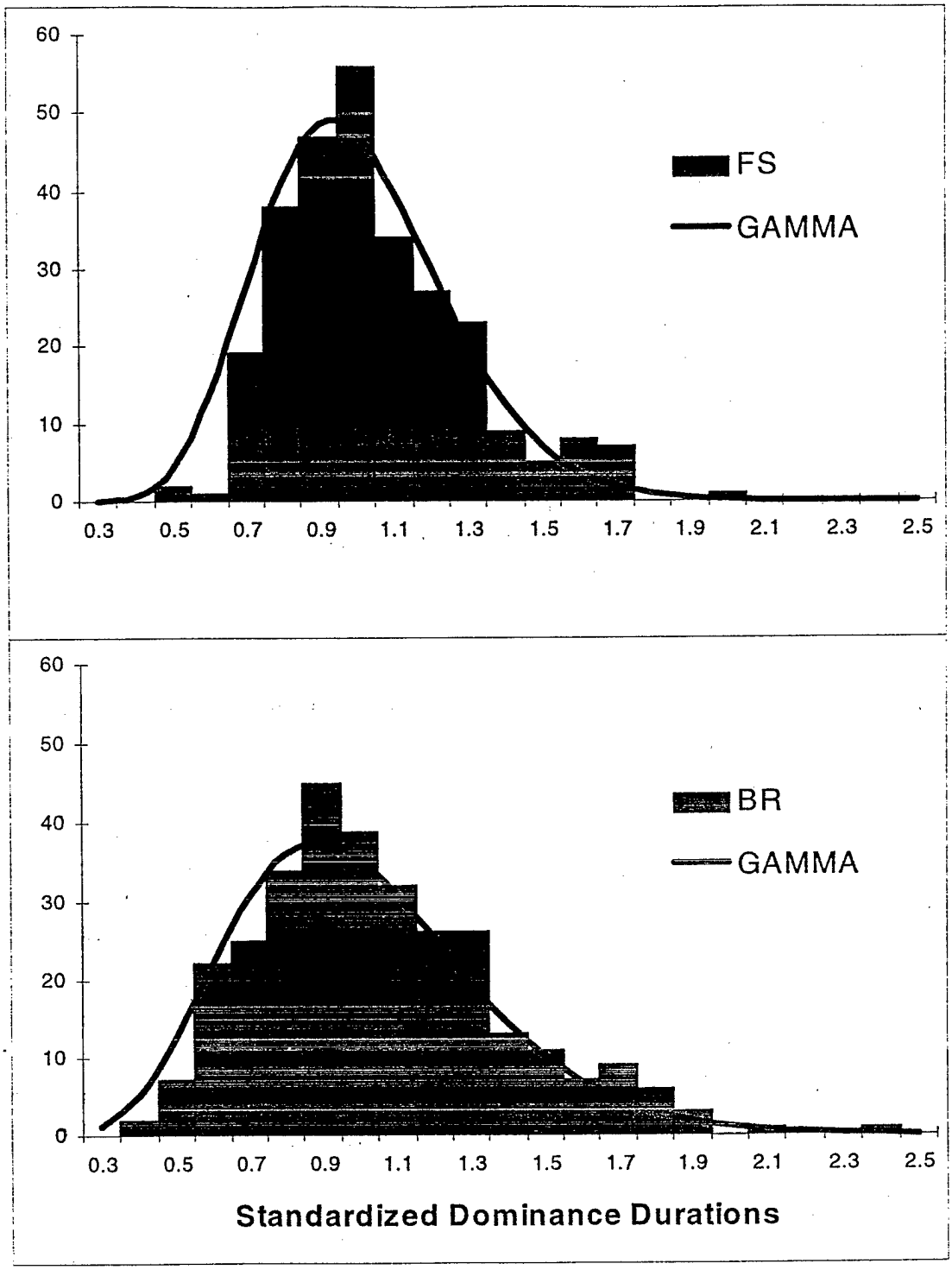

60
50
40
30
20
10
0
0.3
0.5
0.7
0.9
1.1
1.3
1.5
1.7
1.9
2.1
2.3
2.5
FS
GAMMA
BR
GAMMA
Standardized Dominance Durations

Figure 6.

The observed distribution for FS is different from that for BR (Chi-Square goodness of fit: 51.63, $p<.001$). This difference possibly arises from the smaller varience of durations seen in FS. The cumulative percent frequency distributions for BR and FS are correlated ($R^2=.99$). Additional studies are needed to better classify the relation between FS and BR durations, but the observation that they both are reasonably well described by the gamma distribution suggests they are mediated by the same mechanism.

Masking

The flash suppression experiments presented below involve stimulus presentations that resemble some experimental paradigms that fall under the broad term masking. Several reviews of masking studies illustrate similarities and differences between masking and FS (Breitmeyer and Ganz, 1976; Kahneman, 1968; Turvey, 1973). Visual masking occurs when two stimuli are presented close together in time and space. Forward and backward masking refer to presentation of a mask followed by a test probe (forward) or preceded by a test probe (backward). Paracontrast and metacontrast are subsets of forward and backward masking when the mask and stimulus probe are

contiguous or close together spatially but do not overlap. All FS studies presented below involve stimuli that overlap dichoptically; therefore, para and metacontrast studies would not be strictly comparable.

Although a review of the masking literature reveals quite diverse findings under various conditions, some generalizations can be made when comparing masking to FS. Masking studies usually involve monocularly presented, brief, mask and test probe stimuli (Crawford, 1946; Sperling, 1964), as well as mask and test probes which have similar physical characteristics (Legge, 1979; Switkes, Bradley and DeValois, 1988). In general, dichoptic masking is minimal when mask and test are physically different and presentation is separated over time by more than about 200 msec (Battersby and Wagman, 1962). The flash suppression experiments to follow use very different "mask" and probe stimuli--a grating to one eye and a small spectral increment to the other. In FS, suppression increases with an increase in the presentation time of the two stimuli; an effect opposite of that was found in all classical masking studies.

There are certainly similarities between FS and some masking studies (Schiller, 1965; Turvey, 1973), but there are also considerable differences. Our FS studies use long

duration flashes of a grating to one eye (2000 msec), and the display assumes an appearance like conventional studies of binocular rivalry or permanent suppression (Figure 1). Even if FS shares some mechanisms with what has conventionally been called masking, the time course and magnitude of suppression has not been systematically studied and reported under the FS paradigm. Experiment 5 provides some control experiments designed to identify how much suppression is due to rivalry and how much to masking.

Neurophysiological Studies

A subject viewing a rivalry stimulus like Figure 1 has to be impressed by the disappearance from awareness of a grating that is many times above threshold. Despite this very strong perceptual phenomenon, there has been, until very recently, scarce evidence about the neural origin of the suppression (Sloane, 1985). Prevailing neural theories posit suppressive interactions early in the visual system--the lateral geniculate nucleus (LGN) or monocular neurons in the striate cortex (Blake, 1989; Lehky, 1988; Lehky and Blake, 1990). Varela and Singer (1987) did show orientation specific suppression in the LGN of anesthetized cats, but the suppression had a long latency on the order of one second, and there was considerable suppression for many

cells at all orientations, not just orthogonal as would be required for BR. Furthermore, these results could not be replicated by other investigators (Sengpiel, Blakemore, and Harrad, 1994; Moore, Spear, Kim, and Xue, 1992).

Other studies also have failed to find a BR suppression "signature" in the visual cortex (V1) of anesthetized cats (Ohzawa and Freeman, 1986a, 1986b; DeAngelis, Robson, Ohzawa, and Freeman, 1992). These studies tested cortical cells by flashing orthogonal gratings to each eye simultaneously. As described above, simultaneous presentation favors perceptual fusion, at least for the first 150 msec (Wolf, 1983).

A FS procedure was used to produce strong interocular suppression in V1 of anesthetized cats (Sengpiel and Blakemore, 1994; Sengpiel, Blakemore, and Harrad, 1994). Dichoptically presented, orthogonal, drifting, sine wave gratings were used. Suppression was only evident when one eye had already been viewing a stimulus when the orthogonal grating was flashed to the other eye (Wolfe, 1984). This FS was also effective in producing suppression in cat LGN, but the suppression was not orientation selective, which effectively rules out the LGN as the primary site for BR suppression. None of the monocular cortical cells showed

orientation selective suppression whereas about half of the binocular neurons did (Sengpiel et al.).

Neurons in the LGN of alert monkeys are not modulated during viewing of BR targets (Lehky and Maunsell, 1996). These animals were apparently not presented with stimuli in a FS paradigm but with free viewing rivalry stimuli (e.g., BR). Some studies of suppression activity in the visual cortex of alert monkey have been inconclusive. Only a small percentage of cells in area MT (Logothetis and Schall, 1989), and areas V1, V2, V4 (Dobbins, Jeo and Allman, 1994) showed suppression related to subjects' reports of suppression. Other studies have shown a more convincing BR suppression in V1, V2, and V4 (Leopold and Logothetis, 1995) and the inferior temporal cortex (Sheinberg, Leopold, and Logothetis, 1995). A FS technique was used to alter the perceived dominance of stimuli in monkeys and humans (Sheinberg, Leopold and Logothetis, 1995), and strong suppression of the firing rate of many neurons in those alert monkeys was correlated with the FS procedures.

These recent neurophysiological studies, enhanced by FS techniques, have generated a new interest in the neural basis for suppression. Binocular rivalry, flash suppression, and permanent suppression (Figure 1) are

phenomena that can easily be investigated in the laboratory in normal subjects and in those with abnormal clinical suppression. The experiments presented in this dissertation are the only reports to date systematically investigating the time course and magnitude of suppression in a flash suppression paradigm. The results can be compared to older studies of BR and PS and used to establish parameters useful for designing human and animal experiments and neural models of suppression.

METHODS

Apparatus and Stimulus Conditions

Suppression Inducing Stimuli

Stimuli of the type commonly used to induce binocular rivalry (Figure 1) were viewed dichoptically through a Brewster-Holmes type stereoscope (Figure 7). The basic apparatus has been described elsewhere (Ooi and Loop, 1994). Inducing figures were viewed through + 5.25 diopter, base in prism lenses so that figures separated by about 8 - 9 cm, adjusted for each subject, are seen with zero accommodative and vergence demand. The inducing stimuli were high contrast 2.6 cycles per degree (cpd) square wave gratings subtending 6.7 X 6.7 degrees at the eye (Figure 1). The gratings were framed by a one degree thick square or round frame as a fusion lock. These dimensions were calculated by using an empirically determined magnification factor for the stereoscope of 1.27%. Slight adjustments of viewing distance were made by each subject; therefore, the actual dimensions of gratings and stimulus probes vary by not more than 10%. For example, the minimum and maximum grating

Figure 7. Flash suppression apparatus. Xeon light source (A) is controlled by a 5 mm aperture Uniblitz shutter (B) and passed through an aperture stop (C). The intensity of the stimulus probe is controlled by subject by a 4 log ND wedge (D). The wavelength is selected by band pass interference filters at E and focused on the Polacoat screen (G) by lens F. High contrast gratings (H) are placed on the viewer's side of the screen and imaged at optical infinity with zero vergence demand by Brewster-Holmes type stereoscope lenses (I). Presentation of the left eye grating is controlled by a flag shutter (J) mounted on a galvanometer. The background illumination is provided by lamp K and wavelength determined by interference filter at L. The intensity of lamp K is regulated by rheostat control and neutral density filters. For Experiment 5, an oscilloscope monitor was used for the background and to produce the gratings. The monitor was imaged at the plane of the screen (G) by use of a beam splitter.

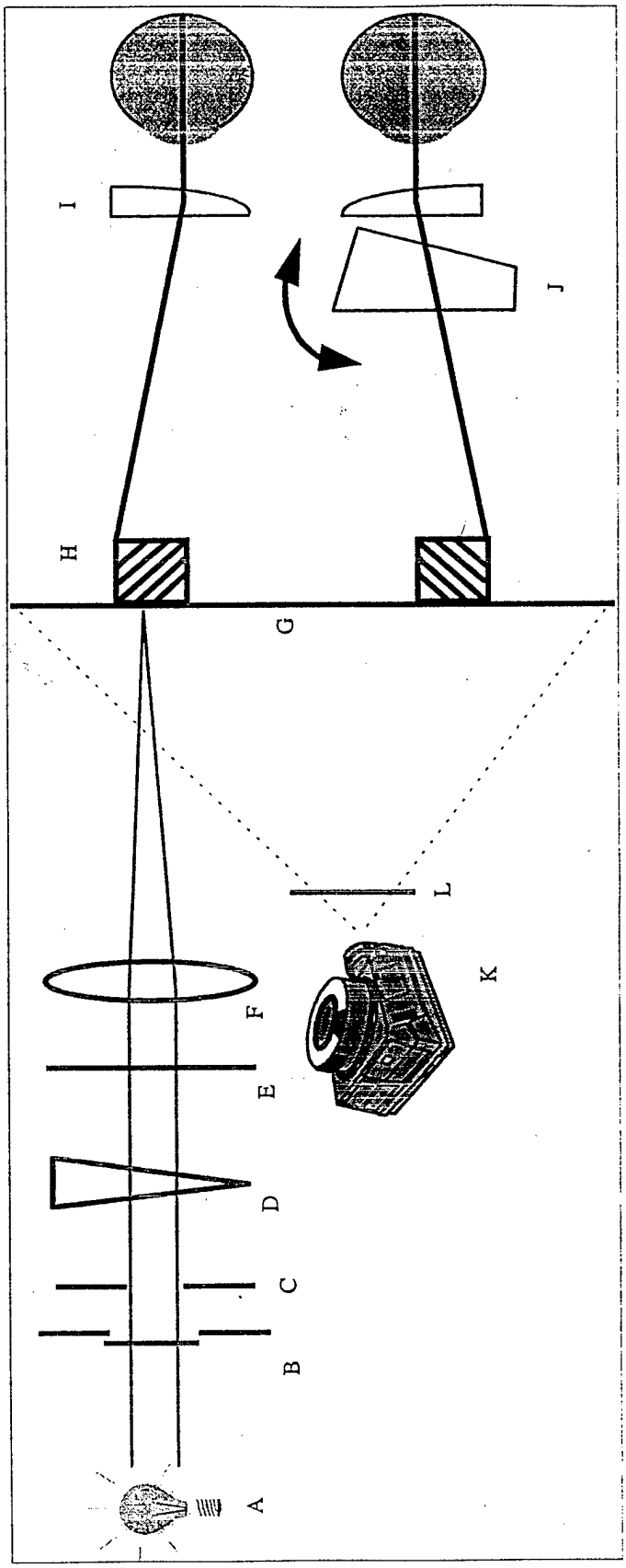


Figure 7.

spatial frequencies resulting from screen adjustments are 2.4 to 2.7 cpd.

All gratings were directly printed on transparent film by a high resolution printer and front mounted on a rear projection screen (3M Polacoat). The contrast of these gratings was about 80%. The background measured 29 X 29 degrees when viewed through the stereoscope.

Probe Stimuli

Threshold intensities or reaction times were determined for round spectral increments (probe) that subtended either 1.2 degrees or 0.2 degrees when viewed on the rear projection screen. The probe duration was adjustable and usually 10, 20, or 100 milliseconds (msec). Wavelengths used were 439 (blue), 540 ("luminance"), 580 (yellow), and 613 (red) nanometers (nm). Bandpass interference filters were used to produce the spectral probes and the 540 nm background. The intensity of the probe was controlled with a 4 log unit neutral density wedge (Kodak, circular). The position of the wedge was monitored by a potentiometer, whose output was displayed on a digital voltmeter and printed for permanent record of threshold settings. Attenuation by the wedge was calibrated independently for each wavelength (Tektronix J6504) in order to account for

any non-linear attenuation of the spectral probe. Log attenuation threshold settings were calculated independently for each wavelength based on a linear regression curve generated from the wedge calibration (R^2 values were > .99 for all wavelengths). The wedge was recalibrated at least twice over a two year period and was consistent within 0.05 log units over a 3.5 log unit range of intensities which includes the range used for all experiments.

Inducing Flash Suppression

The sudden appearance of the flashed grating in the left eye was controlled by a flag shutter mounted on a galvanometer. The left eye view of the grating was occluded by the flag, and when dropped, presented the grating with a rise time of 7 msec as determined with a photocell and oscilloscope. This rise time is comparable to the rise time inherent in a standard 60 Hertz computer monitor. When the left grating appears, the image of the right grating becomes suppressed (Wolfe, 1984; Ooi and Loop, 1994). For Experiment 1, the flag shutter was opaque and when opened, resulted in a large luminance transient in the left eye. For the other experiments, the shutter was translucent and resulted in minimal change in mean luminance when viewing a flashed grating. There was still a small 0.18 log unit

luminance increment in the background because the shutter luminance did not exactly match the background luminance. This luminance transient had minimal effect on the reported results (see Experiment 5, Masking).

The probe can be presented to the right eye being suppressed at various times before or after flashing the left grating. These presentation times are analogous to stimulus onset asynchrony values (SOA) often reported in the visual masking literature. The term "delay" is preferred over SOA and is used in this paper. Probe presentation times relative to the flag shutter were calibrated with a photocell and oscilloscope and are accurate within 9 msec, which represents the fall time of the flag shutter plus a 1 msec rise and fall time of the probe shutter (Uniblitz). All data involve delays of 150 msec before (negative delay) and up to 500 msec after flashing the left eye grating. Some experiments included constant viewing of the left grating (PS), or both gratings (BR), with probe presentation to the right eye.

Oscilloscope Monitor

Experiment 4 included the use of an oscilloscope to generate and present the inducing stimuli (Tektronix 608, Picasso image synthesizer). The apparatus was identical to

Figure 1 except that a beam splitter was placed in front of the rear projection screen and an image of the monitor was superimposed on the screen. The background illumination was controlled by the oscilloscope and was 5 cd/m^2. The square wave grating was 2.6 cpd with a contrast of 60%. The presentation time of the grating with respect to the probe was recalibrated with a second oscilloscope, and delays used were the same as the other experiments. Timing of the grating and probe presentations was controlled with solid state programming modules (Coulbourn).

General Procedures

Threshold Experiments

Procedures unique to each experiment will be covered in more detail as each experiment is presented. This section will outline the general procedure for determining thresholds.

A five minute adaptation to the background preceded each experiment. Thresholds were then determined under dominance and suppression conditions. In the dominance condition, a blue, yellow, red, or green stimulus probe was presented to the right eye in the center of the inducing figure (Figure 1 and Methods). The subject adjusted the intensity of the probe to some criterion level of detection

("color" or "simple detection"). These threshold determinations were repeated under conditions where the same eye was suppressed. Most results are reported simply as the difference between the arithmetic means of dominance and suppression thresholds, in logarithmic units. The logic of the experiments makes unnecessary the reporting of thresholds in absolute units of intensity.

Color Versus Detection Thresholds

Conditions were designed to test effects of suppression on the luminance and opponent-color systems. Simple detection thresholds and discrimination of color thresholds can be measured for the same spectral increment (King-Smith and Carden, 1976). For example, under some test conditions, a red colored probe appears white at threshold while red color is evident at some intensity above threshold. Thus "detection" or "color" thresholds can be determined. To test the opponent-color system, color thresholds were determined by adjusting the intensity of the blue or red probe until the subject could just determine the color of the probe. For testing sensitivity of the luminance system, the subject set thresholds for simple detection of a 540 nm probe presented on a 540 nm background. This arrangement

produces only an intensity change that is detected by the luminance system (Schwartz and Loop, 1982).

The particular wavelengths were chosen after Ooi and Loop (1994). They noted that selection of one short and one long wavelength probe, and a luminance probe was useful for extracting information about spectral sensitivity. Using probes across the entire visible spectrum (Smith et al., 1982) does not add to the results because the only selectivity shown in interocular suppression is in the short wavelengths and between the luminance and opponent-color systems.

Method of Adjustment vs Two Alternative Forced Choice

Regarding concern of possible criterion effects of using a method of adjustment (MAT) for setting thresholds, we compared MAT with a two alternative forced choice procedure (2AFC). Figure 8 and Table 1 shows results for three subjects. MATs were compared to2AFC thresholds during FPS, PS, and FS. For the 2AFC thresholds, a regression line was plotted through the linear portion of the curves and threshold calculated for the 75% correct frequency of seeing. When data for the three subjects are averaged, MAT and 2AFC thresholds are equivalent. Furthermore, the slopes of the 2AFC procedures are similar when comparing dominance

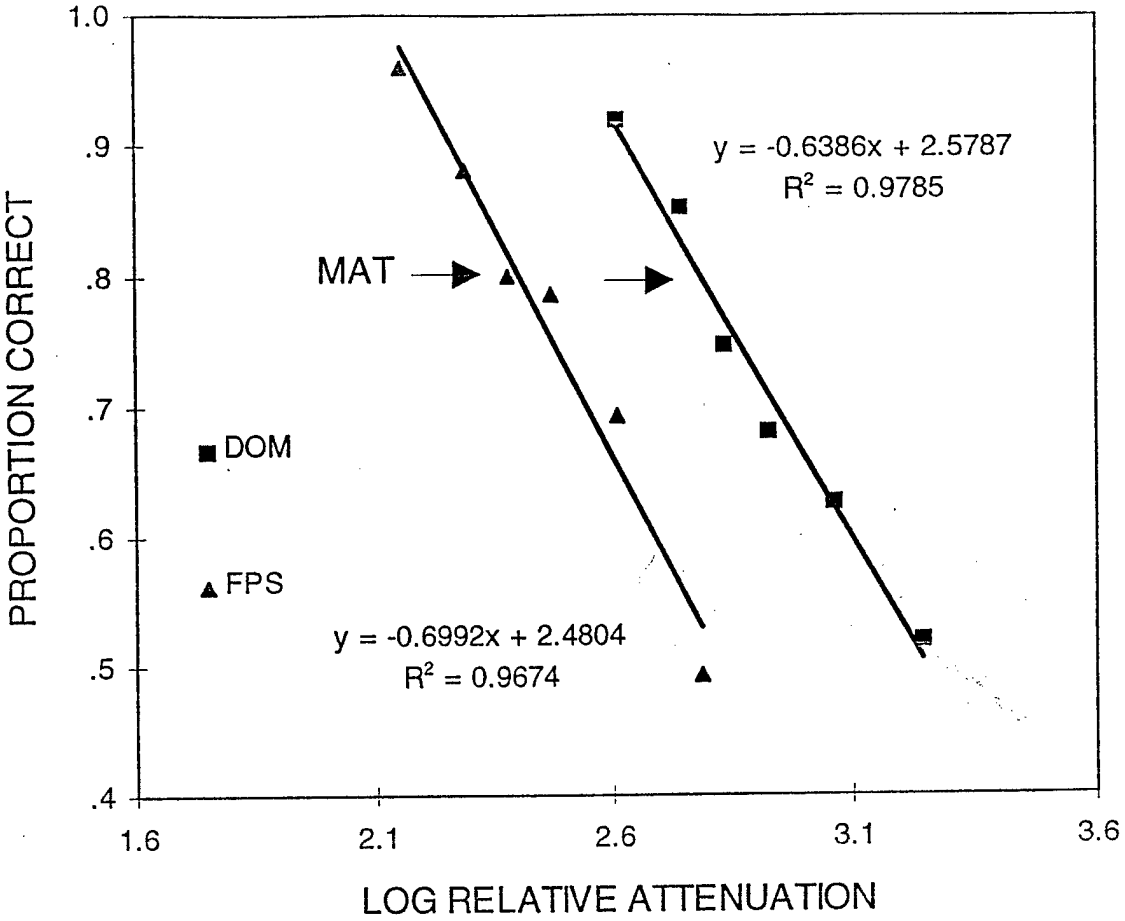


Figure 8. Two alternative forced choice thresholds. Subject KW recorded detectability of a 439 nm, 100 msec, and 1.2 deg probe in a 2AFC paradigm for a range of probe intensities during dominance and suppression. The suppression condition was FPS at a delay of 500 msec. Method of adjustment thresholds (MAT) determined contemporaneously are indicated by arrows. Abscissa is attenuation of probe intensity--smaller numbers = brighter probes.

TABLE 1: Method of Adjustment Versus Two Alternative Forced Choice Thresholds

		Log Sensitivity at MAT	sd	Regression	R^2	% correct at MAT	Log Sensitivity at 75% Correct	Log Suppression Determined By: MAT	2AFC
BB	DOM	2.67 (n=12)	.10	y=-.741x + 2.84	.96	86	2.82	.42	.49
	FPS	2.25 (n=12)	.10	y=-.839x + 2.71	.94	82	2.34		
KW	DOM	2.80 (n=12)	.10	y=-.639x + 2.58	.98	79	2.86	.41	.39
	FPS	2.39 (n=9)	.10	y=-.699x + 2.48	.97	81	2.47		
ML	DOM	2.63 (n=6)	.07	y=-1.18x + 3.84	.85	74	2.62	.57	.49
	FPS	2.06 (n=6)	.07	y=-1.28x + 3.50	.89	85	2.14		
BB	DOM	2.23 (n=6)	.08	y=-1.722x + 4.67	.86	83	2.28	.22	.32
	PS	1.91 (n=6)	.14	y=-1.30x +3.44	.76	95	2.06		
KW	DOM	2.29 (n=6)	.07	y=-.721x + 2.54	.86	89	2.49	.41	.38
	PS	1.88 (n=6)	.04	y=-.672x + 2.16	.96	90	2.10		
ML	DOM	1.78 (n=5)	.09	y=-1.39x + 33.32	.99	85	1.85	.20	.11
	PS	1.58 (n=5)	.09	y=-.731x + 2.02	.95	87	1.74		
BB	DOM	2.19 (n=12)	.11	y=-1.03x + 3.12	.82	86	2.30	.32	.29
	FS	1.87 (n=12)	.21	y=-1.00x + 2.75	.99	88	2.00		

Average FPS (n=3)	.47	.46
Average PS (n=3)	.28	.27

with suppression. "Log Intensity" values are log attenuation of the probe by the ND wedge. These data show that method of adjustment is a reliable method for determining thresholds within this paradigm, and that the observed suppression is not secondary to some criterion effect under the suppression condition.

Flash Suppression (FS)

While viewing a grating with the right eye, an orthogonal grating was repetitively flashed to the left eye with a cycle time of two seconds on and two seconds off. A blue, red, or luminance probe was presented to the right eye with delays of -150 to +500 msec relative to the appearance of the left grating. At least six thresholds were taken for the dominance condition and the suppression condition at each delay, usually over two days with ascending and descending delays counterbalanced over days. Dominance thresholds were always taken before and after each run to average out any effects of adaptation or fatigue.

Permanent Suppression (PS)

A steady state of suppression is produced by viewing a grating in one eye only (Figure 1 and Introduction). Blue, yellow, red, and luminance probes were presented to an eye under dominance and suppression conditions.

Flash Permanent Suppression (FPS)

FPS is conducted under the same conditions as FS except the right eye always views an empty frame on a homogeneous field (Figure 1). FPS allows determining the time course of suppression when presented with a PS stimulus. Blue, red, or luminance probes were presented to an eye under dominance and presented under suppression conditions at various times after onset of suppression.

Binocular Rivalry (BR)

Orthogonal gratings (Figure 1) are viewed continuously and the subject signals when one eye is dominant or suppressed. A stimulus probe, triggered by the subject, is presented during periods of dominance or suppression. Blue, red, or luminance probes are presented to the right eye while under dominance and suppression conditions.

Suprathreshold Experiments

Specific details will be included under the section for Experiment 6. In general, reaction times (RT) to the presentation of stimulus probes were used to measure the relative sensitivity to the probes during dominance and suppression. Reaction times to spectral increments become progressively shorter with an increase in intensity until the RTs reach asymptote (Harwerth and Levi, 1978).

Comparison of RTs during dominance and suppression allows determination of the magnitude of suppression, if any, when stimulus probes are above threshold intensities.

Measures of suppression were determined for FS, and FPS. The same apparatus as shown in Figure 7 was used with the addition of a button for the subject to push in a reaction time paradigm. The button was synchronized with an electronic timer (Coulborn) which was started when the probe was presented and stopped when the button was pushed by the subject. RTs were displayed to the nearest millisecond and permanently recorded for off-line analysis. Presentation of the probe was calibrated with a photocell and oscilloscope and was consistent to within 2 msec.

To control for anticipation, the probe was randomly presented with an a priori probability of 50%. A tone was present 400 msec before presentation of a probe and was also present on the 50% of trials when no probe was presented. Feedback was not given. A second button was used to indicate when the probe was not seen; therefore, RTs were recorded only for probes the subject could see. This control was necessary because some probes were presented at near threshold intensities as determined with the method of adjustment. Method of adjustment thresholds were earlier

shown to be at about the 85% detection level for subjects tested with a two alternative forced choice technique (Figure 8). To account for button slips, RTs less than 150 msecs or longer than 4 standard deviations of the mean were excluded. Only a few such RTs were discarded. Probe intensities were presented in blocks of 50 using a haphazard order of intensities with 25 to 29 RTs taken for each intensity.

EXPERIMENT 1: FLASH SUPPRESSION OPAQUE SHUTTER

Rationale

Ooi and Loop (1992a, 1994) were the first to report on the magnitude of suppression during flash suppression. Unlike binocular rivalry (Smith et al., 1982), in FS, blue color is suppressed less than red, and there is no difference in the magnitude of suppression between red color and the luminance system (Figure 3). Experiment 1 was designed to test the hypothesis that suppression patterns in FS and BR are different because of timing of the probe presentation as suggested by Ooi and Loop (1994). In the BR condition, the subject triggered the presentation of a probe which was then presented at times presumably ranging from about 200 to 600 msecs after suppression, while in the FS condition, the probe was always presented 50 msecs after flashing the suppression inducing grating. If rivalry suppression takes time to develop, sampling suppression during flash suppression at some time greater than 50 msec after onset should result in a suppression pattern more like binocular rivalry.

Detailed Procedures

Four subjects were used: the author (BB), two subjects from the 1994 study (ML, DM), and one inexperienced observer (SB). All subjects had normal corrected visual acuity and stereopsis. Subjects viewed with the right eye a high contrast 2.6 cpd square wave grating oriented at 45 degrees (see methods). The mean luminance of the grating was 12 cd/m^2. For the dominance condition, color thresholds were taken for round, 1.2 degree increments of 439 and 613 nm light projected on the back of the grating while the left eye was occluded by the opaque shutter. Probe durations were 20 msec. The size of the increment was large enough so that it spanned 3 light bars of the grating. Luminance system thresholds were taken by measuring simple detection thresholds of a 540 nm increment on a 540 nm background. Flash suppression thresholds were taken at delays of 50, 300, and 500 msecs after flashing an orthogonal grating to the left eye. An opaque flag shutter as described in the methods and Figure 7 was used to flash the left grating. For each delay, at least six thresholds were taken for the suppression condition. At least twelve dominance thresholds were taken, half at the beginning and half at the end of a run. Magnitude of suppression was calculated for each

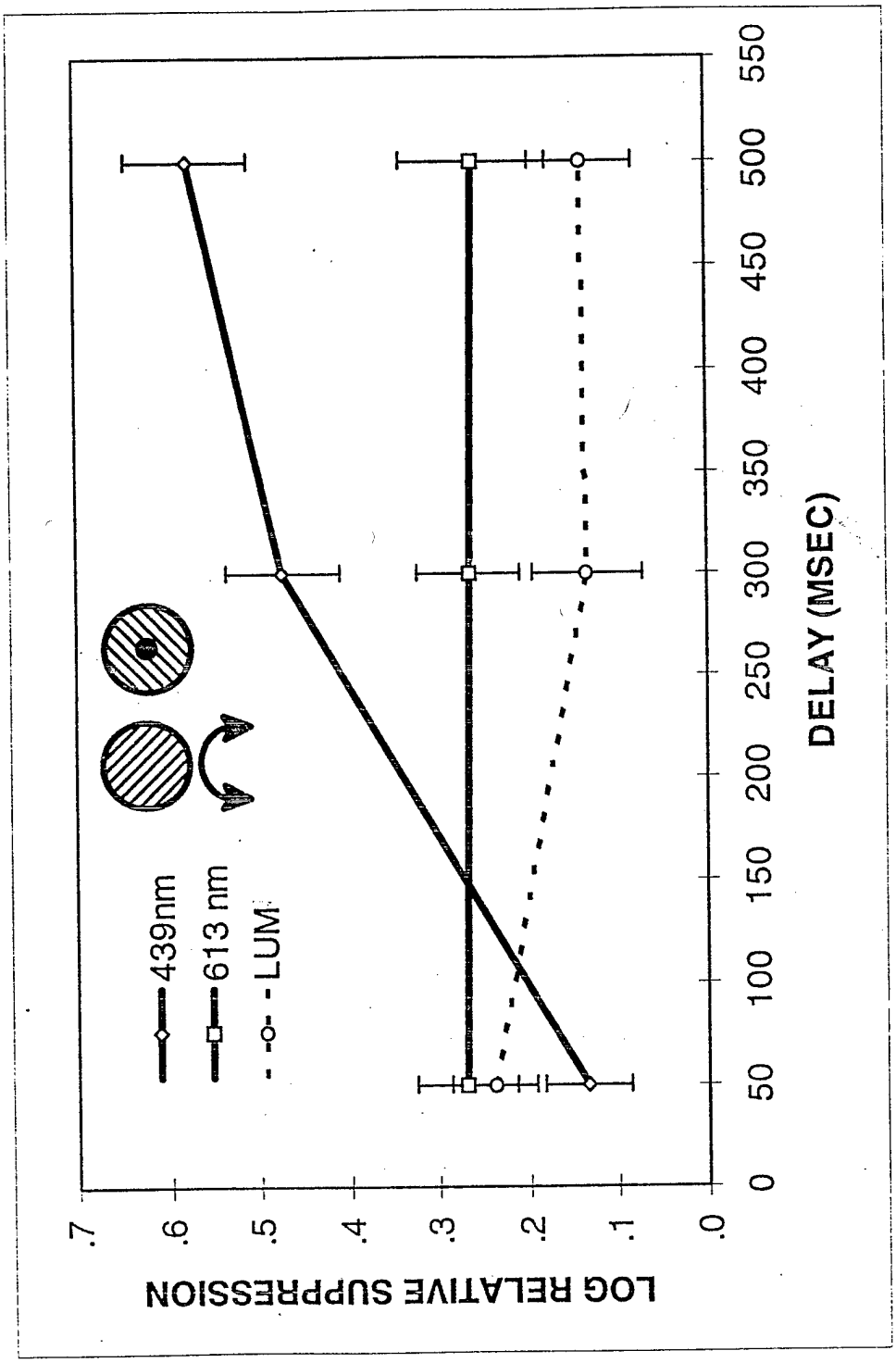
subject by subtracting log attenuation threshold during suppression from log attenuation threshold during dominance.

Results

Data from four subjects are averaged in Figure 9 and show that at a delay of 50 msec, the suppression pattern is similar to that reported in the earlier study of Ooi and Loop (1994) (Figure 3). Blue color is suppressed less, and the red and luminance probes are suppressed about the same. Although there is a trend toward less suppression of the blue probe at delay of 50 msec, the difference is not significant ($F=2.07$, $p=.25$). At longer delays of 300 and 500 msec, when suppression has apparently had time to more fully develop, the suppression patterns of blue, red, and luminance probes look like those reported for BR (Smith et al., 1982; Ooi and Loop, 1992a, 1992b, 1994). At 500 msec, the blue probe is suppressed 0.58 log units, whereas the red and luminance probes are only suppressed 0.26 and 0.14 log units, respectively. At delay of 500 msec, the blue probe is reliably more suppressed than the red and luminance probes ($F=9.09$, $p=.057$).

Figure 10 shows individual results from the four subjects. In all four, the blue probe suppression curve rises considerably over time. Although the relative

Figure 9. Flash suppression, opaque shutter. Average results for four subjects (BB,DM,ML,SB) in a FS paradigm with 20 msec blue (439 nm), red (613 nm), and luminance (540 nm/540 nm bkg) probes. Subjects viewed a 2.6 cpd grating with the right eye, and a probe was delivered at three times (delays) after flashing a grating to the left eye. As in Ooi and Loop (1994), the blue probe is suppressed less than the red or luminance probes at a delay of 50 msec (although this difference is not significant) ($F=2.07$, $p=.25$). There was a reliable repeated measures ANOVA main effects of delay ($F=19.10$, $p=.003$). By 500 msec after suppression onset, the blue probe is suppressed more than the red and luminance probes ($F=9.09$, $p=.057$). Error bars indicate +/- one SEM.


LOG RELATIVE SUPPRESSION
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150
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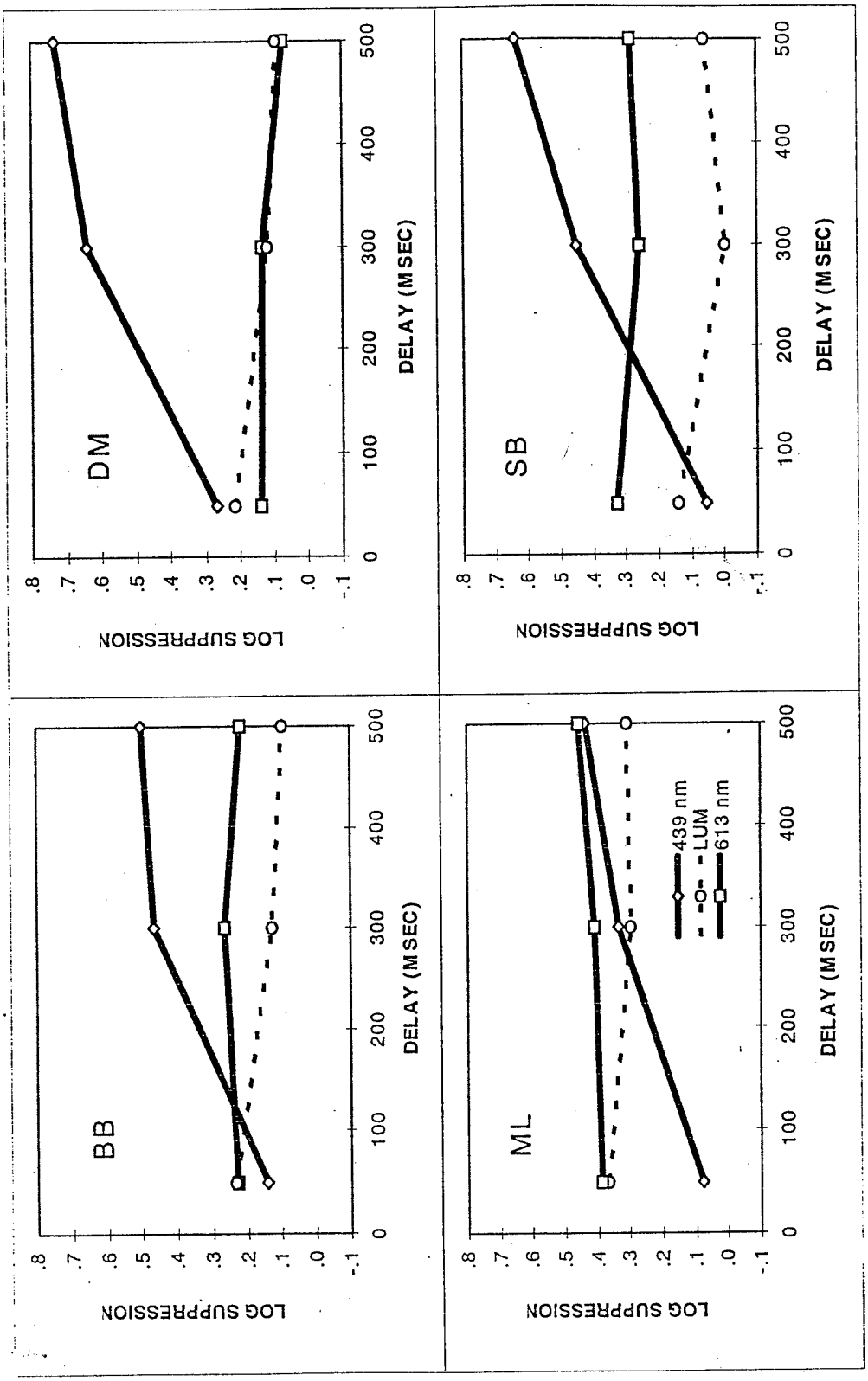
350
400
450
500
550
DELAY (MSEC)
439nm
613 nm
LUM

Figure 9.

Figure 10. FS opaque shutter, subjects. Individual graphs of the four subjects from Experiment 1 (BB,DM,ML,SB). All subjects had an increase in suppression of the blue probe for longer delays.


DM
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ML
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DELAY (MSEC)
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.3
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.1
.0
-.1
0
100
200
300
400
500

Figure 10.

positions of the red and luminance probes are not consistent among subjects, all showed minimal to no change in the magnitude of suppression over time.

An additional control condition was run on three subjects where both gratings were oriented in the same direction. Flashing the same orientation grating resulted in fusion rather than rivalry suppression. Some residual suppression was present and probably represents masking effects from the opaque flag shutter (see Experiment 5: Masking, and Figure 19).

The hypothesis of Ooi and Loop is confirmed. The suppression patterns of blue, red, and luminance probes produced by FS are the same as BR when suppression is sampled at appropriate times after onset(i.e., 500 msec). The observation that suppression in a rivalry situation increases with time is a new finding. Experiments of the type reported by Wolfe (1983) show that fusion gradually develops into suppression over about 100 to 300 msec. But those studies did not look at the actual depth or magnitude of suppression at different times where one eye shifts from dominance to suppression. The only study specifically designed to measure magnitude of suppression over time during BR was conducted in 1972 by Fox and Check. They used

a letter recognition task during the suppression phase of BR and concluded that the magnitude of suppression over a given duration of suppression was constant. Because of limitations in sampling suppression early in BR, Fox and Check were not able to measure suppression at any times earlier than 500 msec after onset. Experiment 2 was designed to take a more detailed look at the time course of suppression in a flash suppression paradigm by sampling suppression during the first 500 msec after onset.

EXPERIMENT 2: FLASH SUPPRESSION AND FLASH PERMANENT SUPPRESSION, TRANSLUCENT SHUTTER

Rationale

Some models of the BR mechanism posit that a neural "switch" causes an instantaneous flip-flop between the states of dominance and suppression (Blake, 1989; Lehky, 1988). Fox and Check (1972) failed to find any difference in magnitude of suppression at different times during probed suppression phases of BR. Their findings support the idea that the visual system instantaneously changes from dominance to suppression. However, due to limitations in precisely following the changes in rivalry state, Fox and Check sampled suppression at times ranging from 500 to 4050 msec after onset of suppression. Sampling times less than 500 msec after suppression onset might be necessary to detect any ramp or rise time of suppression. The results of Experiment 1 did show that the blue probe showed a considerable change in magnitude of suppression over the 450 msec time span tested (Figure 9). The change in magnitude of suppression of the blue probe might be due in part to the

large luminance transient induced by the opaque shutter used in Experiment 1. Also, the early suppression of the red and luminance probes might have been due to effects from the opaque shutter. To minimize any early luminance masking effects, a design change was made to the opaque flag shutter. Experiment 2 was designed to finely sample the magnitude of suppression at times (delays) ranging from 150 msec before to 500 msec after flashing a suppression inducing grating to the left eye.

Experiment 2a: Flash Suppression

Detailed Procedures

The opaque shutter used in Experiment 1 was replaced with a translucent shutter in order to minimize any luminance transient from opening the shutter. The luminance of the translucent shutter (Tektronix J6523) as viewed by the subject, was fortuitously the same as the mean luminance of the left grating to within 0.01 log units. There was, however, a difference in the surround viewed with and without the shutter of 0.18 log units. An additional control experiment using an oscilloscope generated grating showed any masking effect from the translucent shutter to be minimal (See Masking, Figure 21).

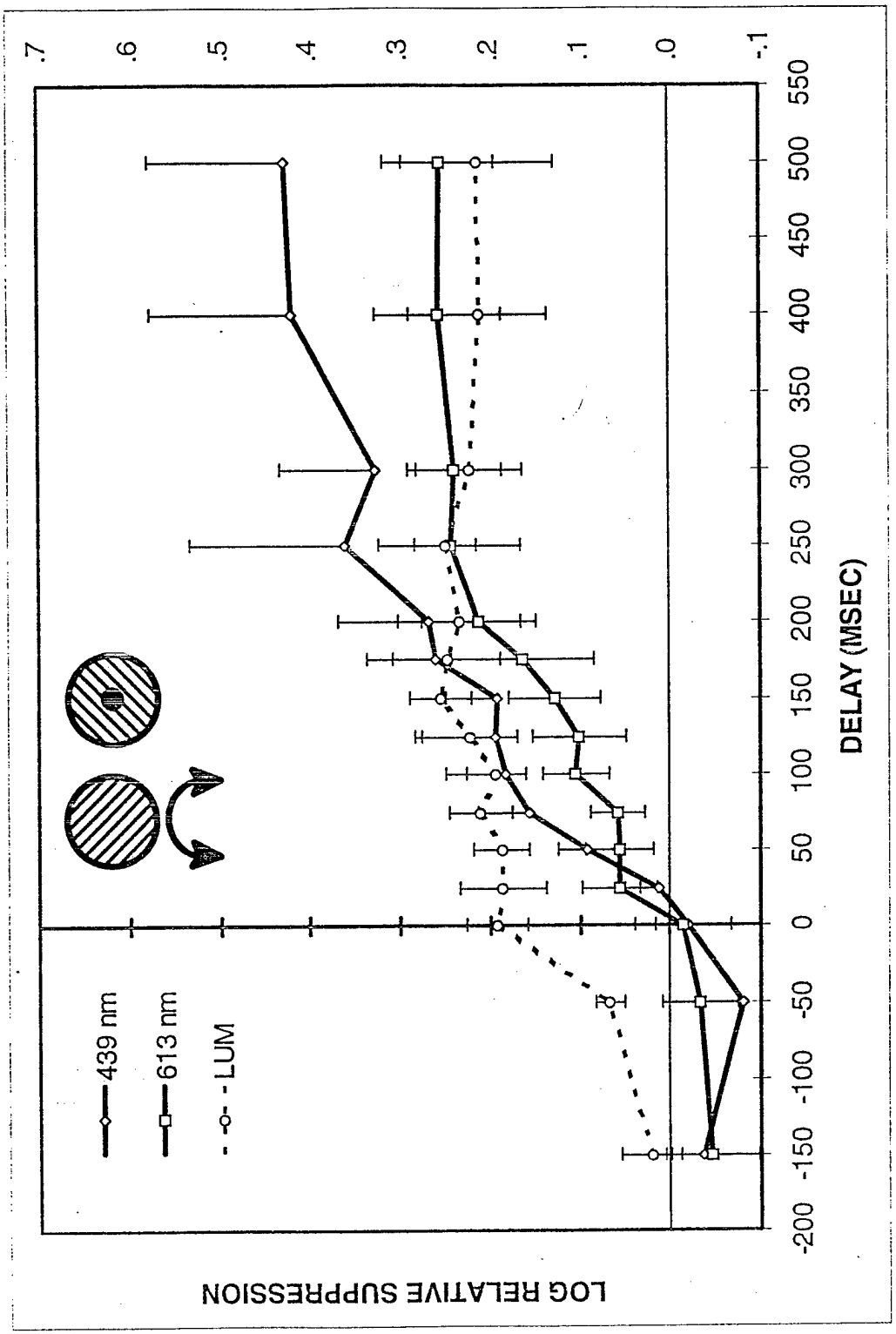
The experimental conditions were the same as Experiment 1 except a translucent shutter was used, more delays were sampled, and a longer probe duration was used. The background was 12 cd/m^2, the grating was a 2.6 cpd square wave, and the probe was a 1.2 degree round increment. The probe duration was 100 msec instead of 20 msec. Early studies using a translucent shutter and 20 msec probes (Baldwin and Loop, 1995) resulted in characteristic rise times of suppression, but the magnitude of suppression was less than that seen when using an opaque shutter. Pilot data had shown that longer probe durations resulted in more suppression, a finding that is explored more completely in Experiment 4.

Subjects included the author (BB), an experienced psychophysical observer (ML), and three inexperienced volunteers (EK, KW, TT). All subjects had normal corrected visual acuity, color vision, and stereopsis. The inexperienced observers practiced at least one day setting color and detection thresholds before data were collected.

Results

Figure 11 shows averaged results for five subjects. Three important observations are apparent in these results. The blue and red probe curves determined by setting "color"

Figure 11. Flash suppression, 100 msec probe. Average of five subjects (BB,EK,KW,ML,TT) in a FS paradigm with 100 msec blue (439 nm), red (613 nm), and luminance (540 nm/540 nm bkg) probes. Subjects viewed a 2.6 cpd grating with the right eye, and a probe was delivered before or after flashing a grating to the left eye using a translucent shutter. There was a reliable repeated measures ANOVA main effects of the interaction between wavelength and delay ($F=43.06$, $p<.001$). At delay of 500, there was a trend toward the same pattern of suppression seen in BR where blue is suppressed more than red ($F=2.88$, $p=.16$) and blue more than luminance ($F=3.75$, $p=.12$). At delay of zero, the luminance probe is suppressed more than the red and blue probes ($F=24.22$, $p=.008$). There is a steady rise time of suppression for the colored probes. Error bars indicate + or - one SEM.


LOG RELATIVE SUPPRESSION
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-100
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0
50
100
150
200
250
300
350
400
450
500
550
DELAY (MSEC)
439 nm
613 nm
LUM

Figure 11.

thresholds, show minimal suppression early and a gradual rise in suppression over the first 200 msec. At 500 msec after suppression onset, the pattern of suppression is similar to previously reported results from BR (Smith et al., 1982; Ooi and Loop, 1994) and FS (Experiment 1) using a 20 msec probe. That is, blue is suppressed most and the luminance probe least. The luminance probe curve, determined by setting simple detection thresholds of a 540 nm increment on a 540 nm background, shows near maximum suppression at zero delay and no change over the following 500 msec.

As seen in Figure 12, there was considerable intersubject variation for FS. However, it is clear that for four of the five subjects, the luminance probe curves are quite flat and the colored probe curves show a rise time of suppression. Subject TT showed minimal suppression for the colored probes. This subject rarely reported suppression of the right grating, but instead said the gratings looked like a plaid or checkerboard after flashing the left grating. TT was the only subject that was not reliably suppressed in these experiments. This subject did show a more typical time course for suppression during FPS (Experiment 2b) but still had lower magnitudes of suppression at longer delays.

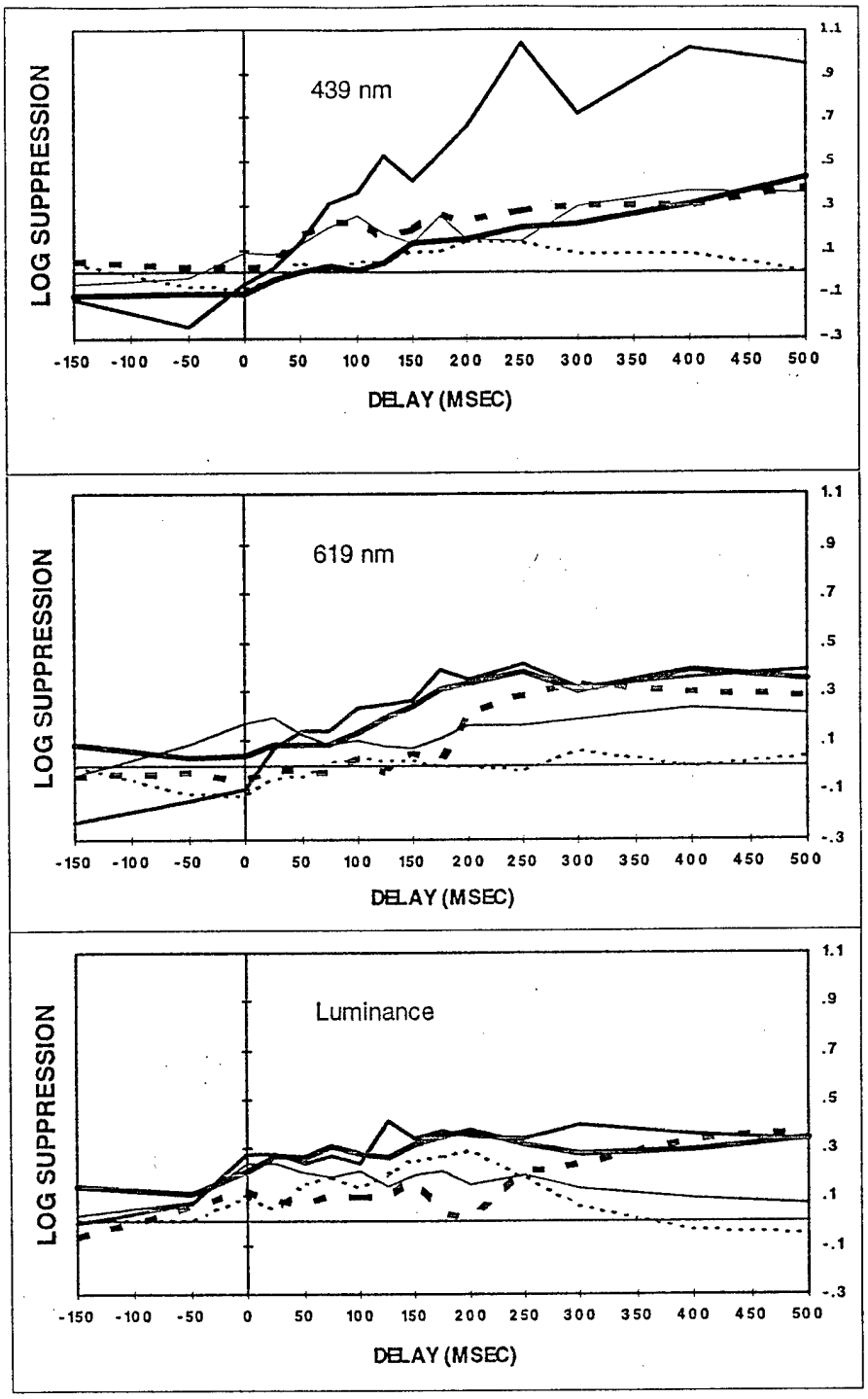


Figure 12. Flash suppression, 100 msec probe, subjects

Subject TT is a helicopter pilot with normal binocular vision and no explanation for his fusion over rivalry was determined. Wolfe (1983) also had one subject that showed only fusion.

One difficulty with studying the time course of suppression with FS is that it must eventually give way to BR. Once the left grating is presented, the subject is thus confronted with BR inducing stimuli and unpredictable right eye switching from suppression to dominance. This is likely the basis for some of the individual variations apparent at the longer delays in Figure 12. For this reason, an experiment using FPS was undertaken to get a clearer picture of suppression time course at its onset.

Experiment 2b: Flash Permanent Suppression

Rationale

A phenomenon related to BR is permanent suppression (Figure 1). PS represents an experimental paradigm that is very useful for exploring the nature of suppression. The stability of the contralateral suppression allows for human subjects and perhaps animals to easily perform tasks required for systematically investigating the nature of suppression. Some authors have argued that PS is not the same as BR (Ridder, Smith, Manny, Harwerth, and Kato, 1972;

Mauk, Francis, and Fox, 1984); others have concluded that PS and BR are the same (Ooi and Loop, 1994; Loop, Baldwin, and Edwards, 1996). If in fact BR, FS, and PS are variations of the same phenomenon, studies using PS and a variation of FS we have called flash permanent suppression (FPS) would allow an easier more efficient way to study rivalry suppression in humans and animals. Experiment 2b was designed to measure the time course of suppression in a FPS paradigm.

Detailed Procedures

The experimental conditions were the same as the FS Experiment 1 except that the right grating was replaced by a homogeneous field upon which a frame serving as a fusion lock was placed to match the frame of the left grating (Figure 1). The luminance of the right field was 12 cd/m^2, which was the same as the mean luminance of the right grating in Experiment 1. The left grating was a 2.6 cpd square wave; the probe size and duration was 1.2 degrees and 100 msec. Dominance thresholds were taken for blue, red, and luminance probes presented in the center of the frame. Suppression thresholds were taken for the same probes but just before or after flashing a grating to the left eye. Subjects included the author (BB), three subjects who

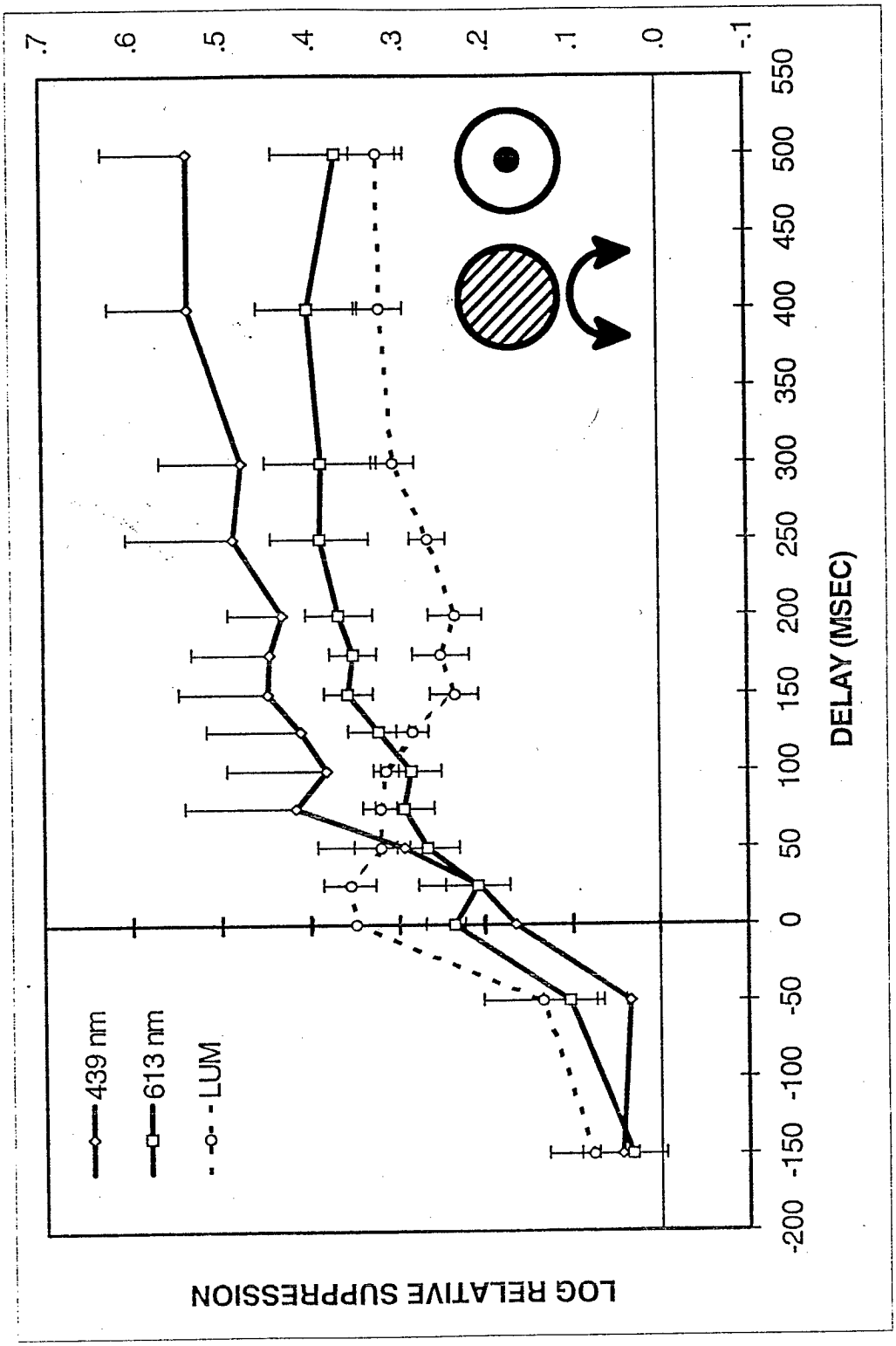
participated in Experiment 2a (EK, ML, TT), and a fifth subject (SB) who participated in Experiment 1.

Results

Figure 13 displays flash permanent suppression functions for the average of five subjects. The general appearance of the suppression patterns are quite similar to those for FS (Figure 11) with the following exceptions. Suppression for the blue and red probes begins earlier and reaches a greater magnitude in FPS. Also, for three of the five subjects, the luminance probe curve takes on a bi-modal waveform. There is less suppression at intermediate delays than at early or late delays. Figure 14 shows less intersubject variation in FPS than in FS (Figure 12).

During FPS, some subjects reported the curious observation that at threshold, in the suppressed condition, the red colored probe appeared red at early and late delays and white at intermediate delays. Experiment 3 was designed to record color and detection thresholds for the same probes and look for any systematic change in the suppression wave forms due to the criterion for threshold.

Figure 13. Flash permanent suppression, 100 msec probe. Average of five subjects (BB,EK,ML,TT,SB) in a FPS paradigm with 100 msec blue (439 nm), red (613 nm), and luminance (540 nm/540 nm bkg) probes. Subjects viewed a homogeneous field with the right eye, and a probe was delivered before or after flashing a grating to the left eye using a translucent shutter. There was a reliable repeated measures ANOVA main effects of the interaction between wavelength and delay ($F=7.24$, $p<.001$). At delay of 500 msec, blue is more suppressed than red and luminance ($F=7,68$, $p=.05$). At delays of zero to 25 msec, luminance is more suppressed than blue and red ($F=6.90$, $p=.058$). The colored probes are suppressed earlier in FPS than in FS (Figure 11). Error bars indicate + or - one SEM.


LOG RELATIVE SUPPRESSION
.7
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.1
.0
-.1
-200
-150
-100
-50
0
50
100
150
200
250
300
350
400
450
500
550
DELAY (MSEC)
439 nm
613 nm
- - -o- - LUM

Figure 13.

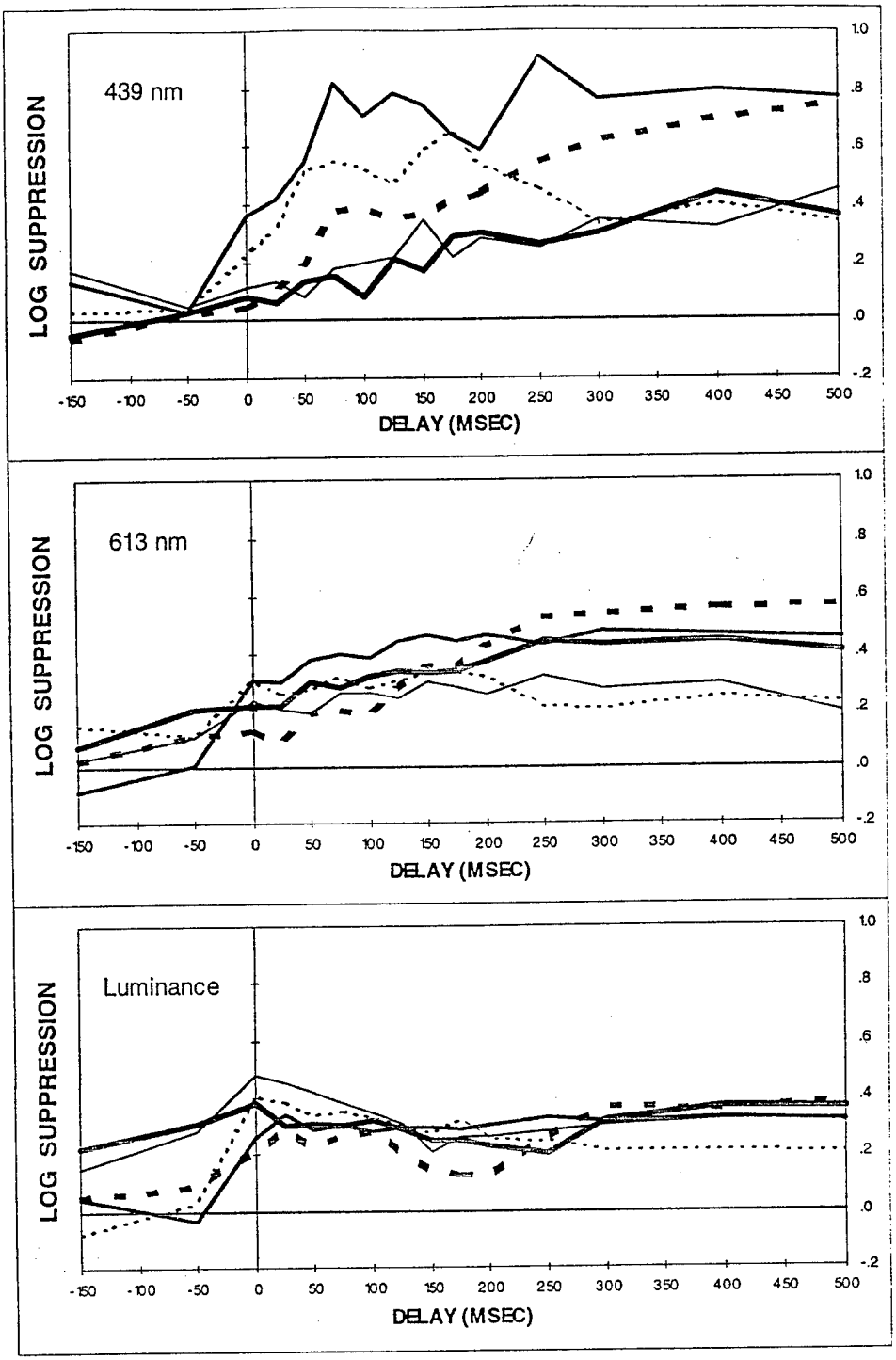

Figure 14. Flash permanent suppression, 100 msec probe, subjects

EXPERIMENT 3: FLASH PERMANENT SUPPRESSION, COLOR VERSUS DETECTION THRESHOLDS

Rationale

Detection of a spectral increment can be mediated by either the opponent-color system or the luminance system. For example, conditions that include a bright background luminance, large probe size, and long probe duration favor detection by the opponent-color system. Spectral probes seen under these conditions appear colored at threshold (King-Smith and Carden, 1976). Changing the conditions to include a dim background and a small, brief probe favors detection by the luminance system. Under these conditions, some wavelengths will appear achromatic at threshold intensities. An experiment can be designed so that at threshold intensity, a spectral increment probe appears achromatic at some intensities and colored at higher intensities, indicating that the luminance system is more sensitive at threshold. During FPS, several subjects reported that at some delays, the red probe appeared white and at other delays, the same probe appeared red. This observation suggests that the luminance and opponent-color

systems are suppressed each with a different time course, the luminance system being suppressed more at short delays and the opponent-color system suppressed more at longer delays. To examine this phenomenon, color and detection thresholds were determined during FPS for red 20 msec probes. Results from pilot studies had indicated that there was a larger split between color and detection thresholds for 20 msec probe durations.

Detailed Procedures

The experimental conditions were identical to experiment 2b FPS except that 20 msec probes were used and subjects recorded detection thresholds on some runs and color thresholds on others. Subjects recorded both color and detection thresholds for the same 613 nm probe but with color and detection thresholds taken on different days. Subjects were BB, KW, and ML, used in earlier experiments, and DE, an inexperienced volunteer. All subjects had normal corrected visual acuity, color vision, and stereopsis.

Subjects set detection thresholds by increasing the intensity of the probe, from non-seeing to seeing, until the probe was just detectable. Color thresholds were set by increasing the intensity of the probe until the subjects could just discriminate the color of the probe.

Results

All subjects had similar findings, and the averaged results are shown in Figure 15. Color thresholds continue to slowly rise over the course of 75 to 500 msec. Detection thresholds run close to color thresholds until about 150 msec, where detection thresholds get better (e.g., are less suppressed) There was a reliable repeated measures ANOVA main effect of the interaction between threshold criteria and delay ($F=3.19$, $p=.002$). Furthermore, there was a significant difference between color and detection thresholds between delays of 175 - 500 msec ($F=10.97$, $p=.045$).

These results mirror subject observations that at longer delays in the suppressed condition, the red probe is seen as an achromatic flash of light and the intensity of the probe must by increased about 0.1 log unit in order to discriminate the red color. These data seem to show a different time course for suppression of the luminance and opponent-color systems. The luminance system is suppressed early after the onset of suppression, and the opponent-color system is suppressed later.

Detection thresholds for luminance probes of six subjects were averaged and taken as a template for the time

Figure 15. Color versus detection thresholds. A. Average of four subjects (BB,DE,KW,ML) in a FPS paradigm with 20 msec, 1.2 deg, red 613 nm probes. Subjects viewed a homogeneous field with the right eye, and a probe was delivered before or after flashing a 2.6 cpd grating to the left eye. Suppression was determined during dominance and suppression with two different threshold criteria. For "color" thresholds, the subject increased the intensity of the probe until red color was detected. For "detection" thresholds, the subject increased the intensity of the probe until it was just detectable. There was a reliable repeated measures ANOVA main effect of the interaction between threshold criteria and delay ($F=3.19$, $p<.002$). There was a significant difference between color and detection thresholds between delays of 175 - 500 msec ($F=10.97$, $p=.045$). B. A luminance system template (average of 6 subjects FPS, 100 msec, 1.2 degree luminance probe) fits the detection thresholds for the red probes at the longer delays. Error bars indicate +/- one SEM.

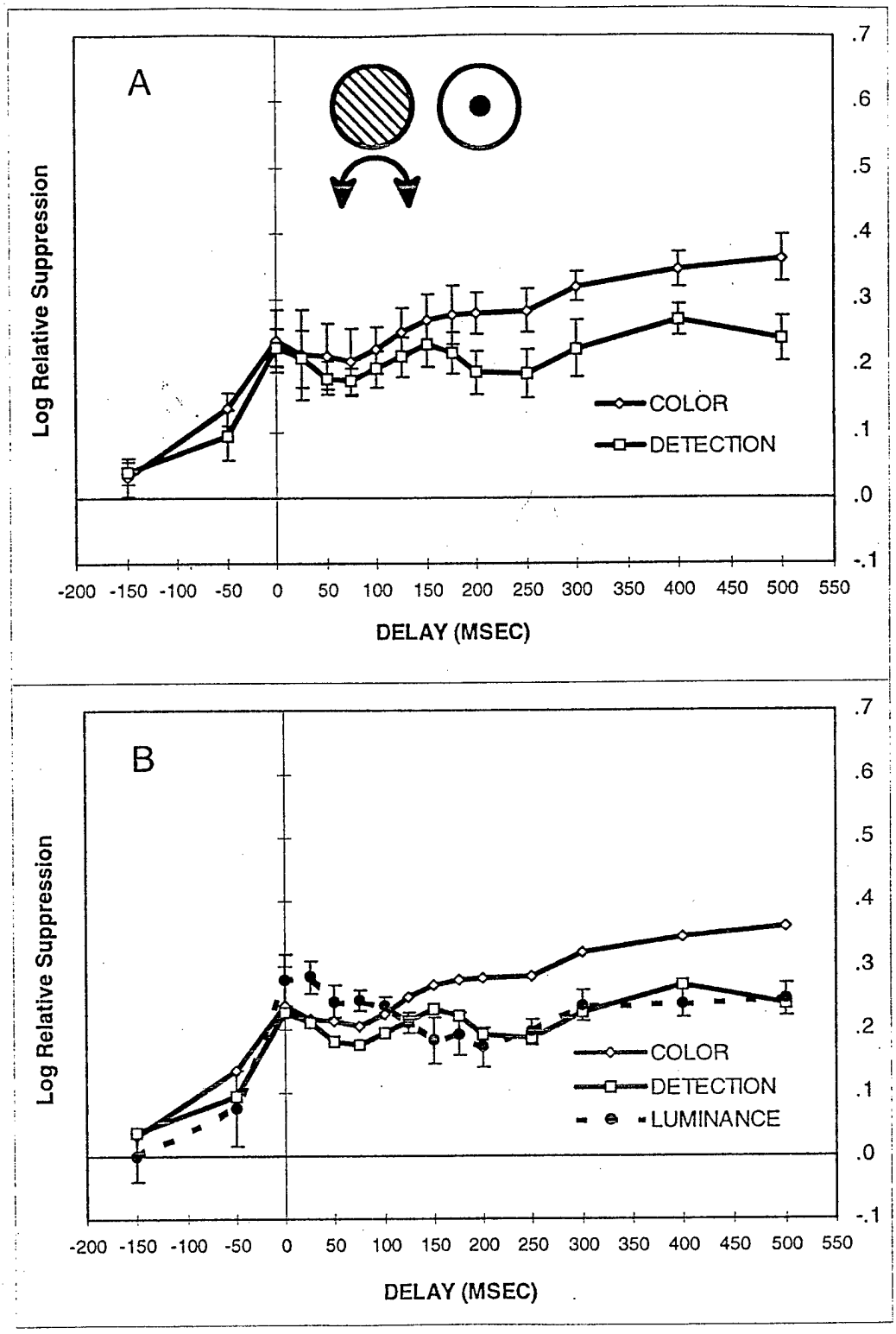
A
Log Relative Suppression
.7
.6
.5
.4
.3
.2
.1
.0
-.1
-200 -150 -100 -50 0 50 100 150 200 250 300 350 400 450 500 550
DELAY (MSEC)
COLOR
DETECTION
B
Log Relative Suppression
.7
.6
.5
.4
.3
.2
.1
.0
-.1
-200 -150 -100 -50 0 50 100 150 200 250 300 350 400 450 500 550
DELAY (MSEC)
COLOR
DETECTION
LUMINANCE

Figure 15.

course of suppression of the luminance system. This template (dashed curve Figure 15), adjusted down 0.07 log units, fits the red probe detection curve quite well over the range of delays from 200 to 500 msec. Notice that at 0 delay, the luminance system is maximally suppressed, which agrees with subject observations that the probe looks red. This also suggests that the opponent-color system is primarily responsible for detection of the red probe early and the luminance system late.

EXPERIMENT 4: EFFECT OF PROBE DURATION AND SIZE

Rationale

The prevailing view that binocular rivalry suppression is non-selective to stimulus attributes (Fox 1991) must be modified to include color versus luminance and wavelength selectivity (Smith et al., 1982; Ooi and Loop, 1994). Pilot studies suggested that the magnitude of suppression during FS, PS, and FPS was also selective for stimulus probe duration. There is no reason, a priori, to think that probe duration should show any selectivity during interocular suppression. For example, our threshold measurements simply compare method of adjustment thresholds during dominance and suppression where all other conditions are the same. Changing the probe duration would still require comparing sensitivity to the same probe under dominance and suppression. In fact, several studies of BR varied probe durations between subjects, as a way of varying flash brightness, without regard to any possible differential effect from the probe duration itself (Blake and Camisa, 1978; Blake and Fox, 1974). We do know from Smith et al. that BR suppresses the opponent-color system

more than the luminance system, and the same holds true for PS (Ooi and Loop, 1994; Loop, Baldwin, and Edwards, 1996). This suggests that a short duration probe, which favors detection by the luminance system (King-Smith and Carden, 1976), might be suppressed less than a longer duration probe that is processed by the opponent-color system. To our knowledge, there has never been a systematic investigation of the effect of probe duration on interocular suppression.

In Experiment 4a, we have measured the magnitude of suppression during PS for 1.2 degree, colored, and luminance probes for duration ranges from 10 to 640 msec. In Experiment 4b, we ran flash permanent suppression conditions using a small, brief probe of 0.2 degrees, 10 msec duration. The results are compared to earlier experiments and show considerable influence on the time course and magnitude of suppression with changes in duration and size of the probe.

Experiment 4a: Permanent Suppression

Detailed Procedures

Three subjects used earlier (BB,DE,ML) recorded detection thresholds for 1.2 degree probes of wavelength 439 nm, 580 nm, and 613 nm projected on an achromatic background of 12 cd/m^2. Detection thresholds were also recorded for luminance probes consisting of 540 nm increments on a 540

nm, 12 cd/m^2 background. The permanent suppression (PS) condition was used to generate suppression, where a homogeneous field is viewed with the right eye and a grating viewed continuously with the left eye. Durations used for the blue, red, and luminance probes were 10, 20, 40, 60, 80, 120, 160, and 320 msec. Durations for the yellow 580 nm probes were 10, 20, 40, 80, 160, 320, and 640 msec. A total of six thresholds were recorded at each duration for both dominance and suppression with ascending and descending durations counterbalanced across two days. For a given duration, a subject's average suppression threshold was subtracted from the dominance threshold and the result reported as log relative suppression.

Results

All three subjects showed the same trends, and the three subject averages are shown in Figure 16. Several important observations can be made from these data. The blue probe is suppressed most at all but the longest durations. The slope of the blue curve is quite flat indicating that probe duration has little effect on the magnitude of suppression presumably because color is suppressed most and blue is always detected as a color. The 580 and 613 nm probes are unaffected by changes in probe

Figure 16. Effect of probe duration on permanent suppression. Average of three subjects (BB,DE,ML) in a PS paradigm with blue (439 nm), yellow (580 nm), red (613 nm), and luminance (540 nm/540 nm bkg) probes. Subjects viewed a homogeneous field with the right eye and a 2.6 cpd grating with the left eye. Probes over a range of durations were presented to the right eye, and "detection" thresholds were taken in dominance and suppression. A reliable repeated measures ANOVA main effect of color ($F=8.66$, $p=.04$), and duration ($F=5.21$, $p=.004$) was seen for the blue, red, and luminance probes. Data for the yellow probe curve was collected in an additional experiment and added to the chart for comparison. Error bars indicate + or - one SEM.

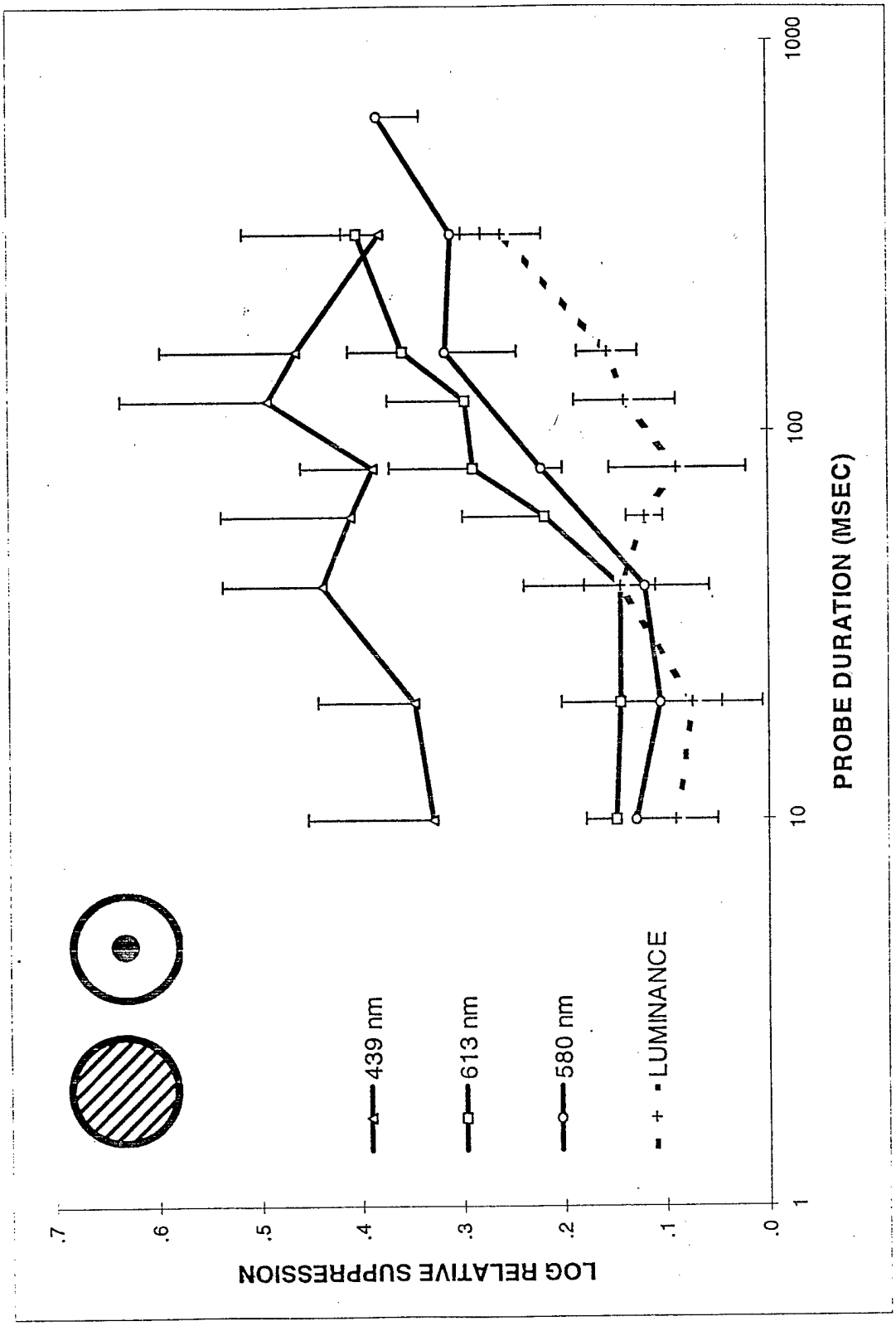
LOG RELATIVE SUPPRESSION
.7
.6
.5
.4
.3
.2
.1
.0
1
10
100
1000
PROBE DURATION (MSEC)
439 nm
613 nm
580 nm
+ - LUMINANCE

Figure 16.

duration from 10 to 40 msec, but the magnitude of suppression increases with probe durations longer than 40 msec. This is presumably due to the fact that at short durations, these probes are first detected by the luminance system (King-Smith and Carden, 1976),, but as duration increased, color is first detected and therefore more suppression ensues. The luminance probe is suppressed the least but does, somewhat surprisingly, increase in magnitude for the longest probe durations.

Our conditions of moderate background intensity (12 cd/m^2) and short probe durations favor detection by the luminance system, and predictions that luminance probes are suppressed less is confirmed. The luminance probe was designed to isolate detection by the luminance system (Schwartz and Loop 1982). Even the luminance probe shows increasing suppression at long durations, which is not expected if the luminance system is always minimally suppressed. Perhaps our luminance probe does not completely isolate the luminance system at longer durations, or there may be some unspecified interactions or limitations to processing of long duration probes by the luminance system.

Under ordinary experimental conditions, short wavelength stimuli do not participate in the luminance

system (Stockman, MacLeod and DePriest, 1991). Since the opponent-color system is suppressed more during PS, it is not surprising to see more suppression of the 439 nm probe and little effect from duration. The pattern of suppression (B>R>LUM) at a duration of 20 msec is consistent with other reports of PS (Ooi and Loop, 1994; Loop, Baldwin, and Edwards, 1996). Following the curves out to durations longer that 600 msec, it appears that at some very long durations, on the order of one second, all probes would be equally suppressed. Two subjects (BB,DE) recorded additional thresholds for the 439 nm probe at a duration of 1200 msec, and the average suppression was 0.41 log units, which would not increase the slope of the blue curve.

The reason for the increase in magnitude of suppression for longer probe durations is apparent in Figure 17. Log attenuation thresholds for blue, yellow, and luminance probes are plotted for all durations tested in both dominance and suppressed conditions. For this subject (DE), temporal summation for the luminance probe and the 580 nm probe was complete at about 60 - 120 msec in the suppressed condition. However, in the dominance condition, there were still small increases in sensitivity for the longest durations tested, so temporal summation was not complete.

Figure 17. Temporal summation during permanent suppression. Data from subject DE. Thresholds were determined during dominance and PS for blue (439 nm), yellow (580 nm), and luminance (540 nm/540 nm bkg) probes. The ordinate shows log attenuation (by ND wedge) of the probes at threshold. Larger numbers indicate dimmer probe intensities thus better thresholds. The abscissa shows duration of the probe on a logarithmic scale. Note that for the luminance and yellow probes, during PS, increases in probe duration beyond 60 msec (yellow) and 120 msec (luminance), do not improve thresholds; whereas, in the dominance condition, increases in duration result in small improvements in threshold out to the longest durations tested.

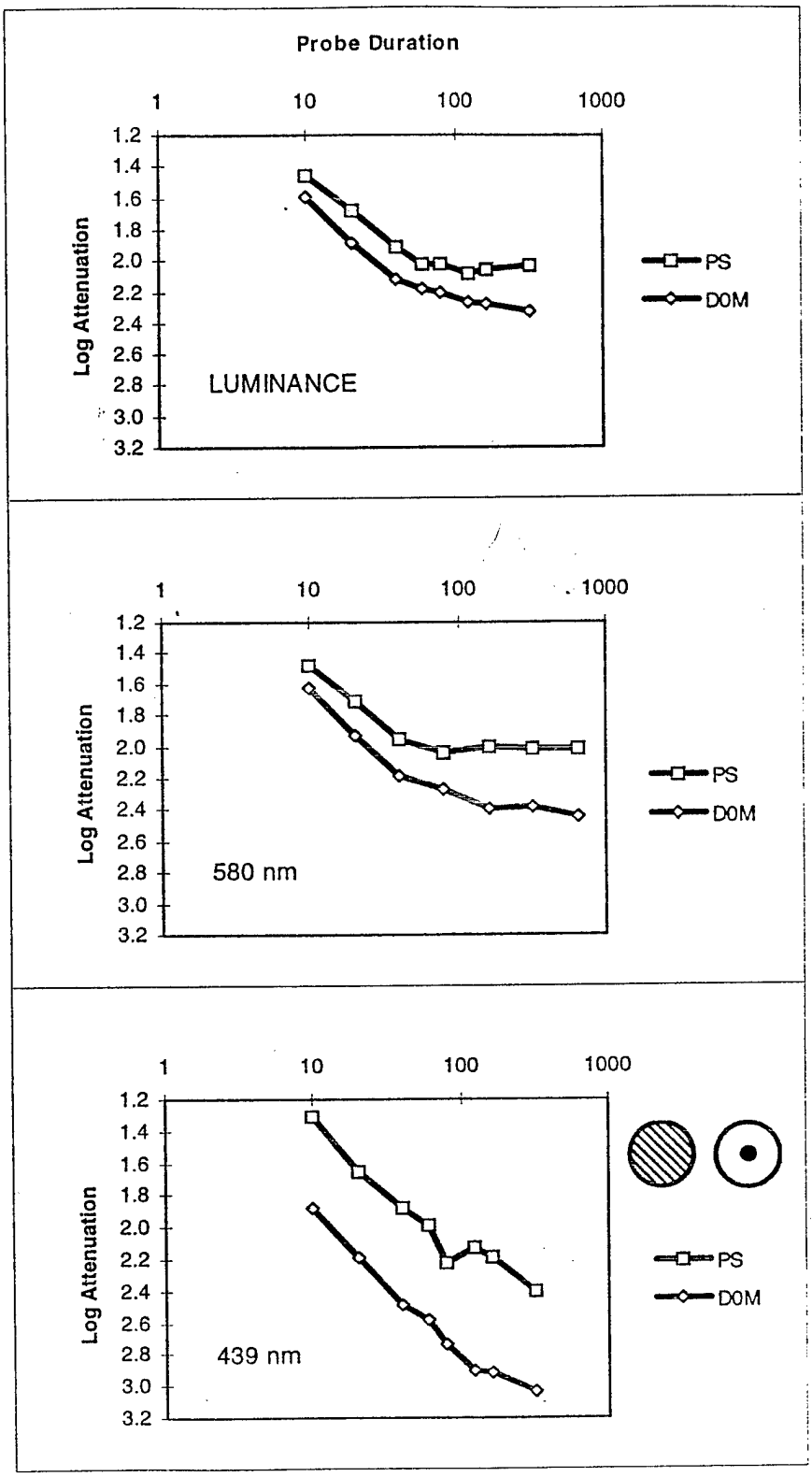
Probe Duration
1
10
100
1000
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
Log Attenuation
LUMINANCE
PS
DOM
580 nm
439 nm

Figure 17.

For the short wavelength probe, temporal summation was not complete for dominance nor for suppression at the durations tested, and the curves are more parallel thus generating a suppression curve (Figure 16) with a nearly flat slope. The other two subjects had results similar to Figure 17 for PS. Additionally, two subjects also showed similar temporal summation trends for both color and detection thresholds taken during flash permanent suppression (data not shown).

These results suggest that some interactive process during interocular suppression reduces the ability of the visual system to temporally integrate the visual information available in these increment stimuli probes. There is no such impairment during dominance, therefore, the greater magnitude of suppression for longer duration probes is due to shortened temporal summation times during suppression.

Experiment 4b: Flash Permanent Suppression, Small Brief Probe

Detailed Procedures

Three subjects (BB, DE, ML) recorded color thresholds for 439 nm and 613 nm probes and detection thresholds for a 540 nm probe under FPS conditions that were otherwise the same as Experiment 2b. The probe was restricted to 0.2 degrees by use of a precision pinhole placed near the

electronic shutter aperture. The probe duration was a ten millisecond square wave as described in the Methods.

Results

Figure 18 shows averaged results for the three subjects. The red and luminance probes showed minimal to no suppression for the first 200 msec after appearance of the flashed left grating. The average magnitude of suppression for the three subjects did not exceed 0.1 log units. The blue probe, on the other hand, still showed considerable suppression for two of the three subjects although the magnitude was considerably less than with the 1.2 degree, 100 msec probe used in Experiment 2. These results are consistent with the view that small brief probes are processed by the luminance system and the luminance system is little affected by interocular suppression. The remaining blue probe suppression is presumably due to a blue color mechanism mediating detection of the 439 nm probe. Additionally, the 0.2 degree probe is smaller than the zone of the human fovea (0.35 degrees) that is free of blue cones (Curcio, Allen, Sloan, Lerea, Hurley, Klock, and Miliam (1991). Perhaps suppression of the blue probe is related to unsteady fixation and a paucity of blue cones in the fovea.

Figure 18. Flash permanent suppression, 0.2 degree probe. Average of three subjects (BB,DE,ML) in a FPS paradigm with blue (439 nm), red (613 nm), and luminance (540 nm/540 nm bkg) probes. Subjects viewed a homogeneous field with the right eye, and a probe was delivered before or after flashing a 2.6 cpd grating to the left eye. Probe duration was 10 msec. Error bars indicate +/- one SEM.

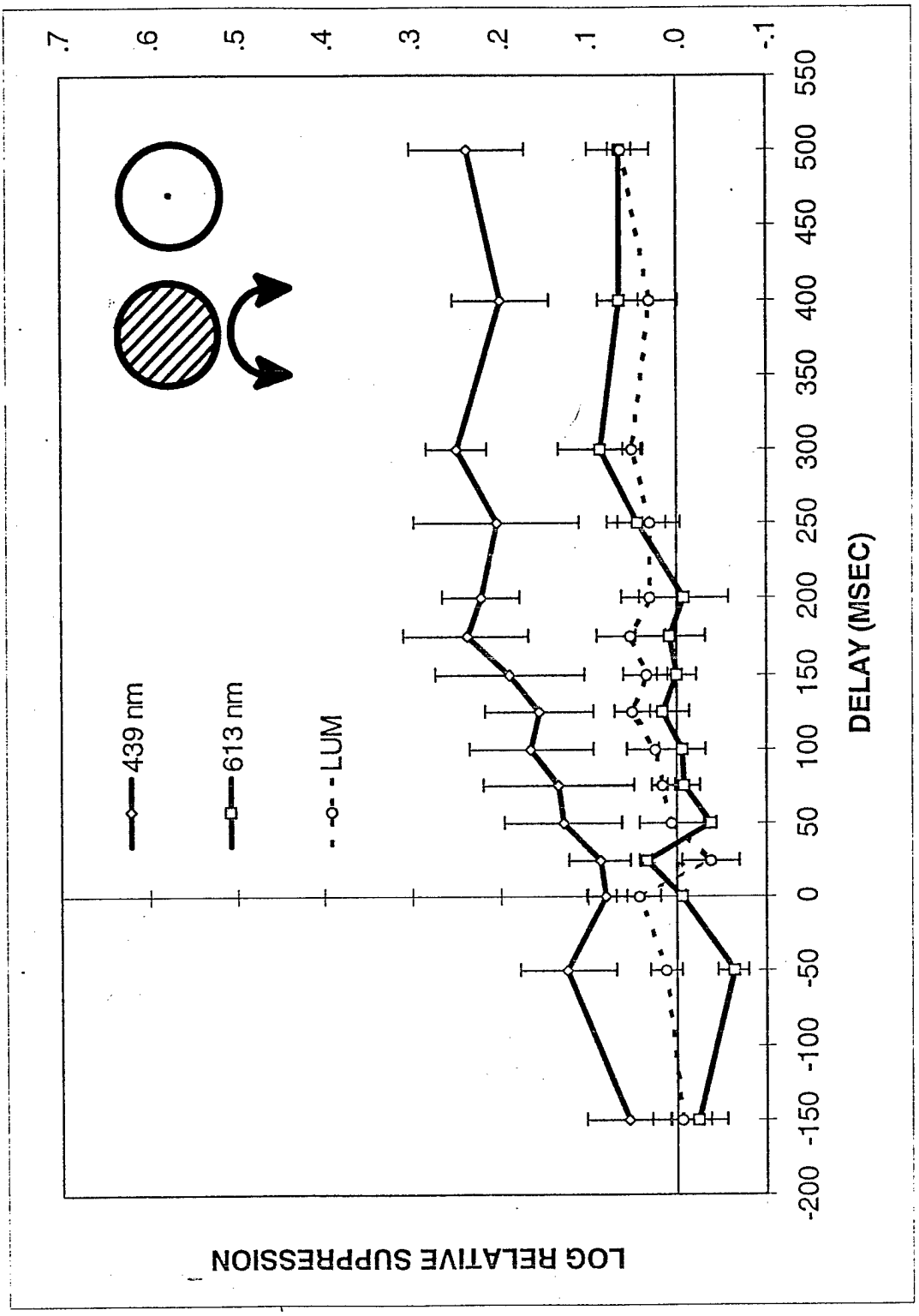
LOG RELATIVE SUPPRESSION
.7
.6
.5
.4
.3
.2
.1
.0
-.1
-200 -150 -100 -50 0 50 100 150 200 250 300 350 400 450 500 550
DELAY (MSEC)
439 nm
613 nm
LUM

Figure 18.

An alternative explanation for the lack of suppression for the red and luminance probes (Figure 18) is spatial interaction between the grating and the probe. As reviewed in the Introduction, Kaufman (1963) and Liu and Schor (1994) have shown that there is a limit to the spatial zone of suppression produced by the bars of a grating. The large, 1.2 degree probe in Experiments 1 - 3 spans three cycles of the grating, whereas the 0.2 degree probe of Experiment 4 fits between two dark bars. If there is a limit to the spatial zone of suppression between the bars of our 2.6 cpd grating, then the tiny probe might be located in a zone of less suppression. This is unlikely because both Kaufman, and Liu and Schor have shown that the suppression zone for a 2.6 cpd grating is much larger than the distance between two dark bars and is in fact on the order of one degree.

EXPERIMENT 5: MASKING CONTROLS

Rationale

Experiments 1 - 4 used a flag shutter to control the presentation of the suppression inducing grating. In Experiment 1, the shutter was opaque; therefore, when opened, the left eye saw a large transient increase in luminance on the order of 3 log units. Over concern about possible masking effects from this luminance transient, a translucent flag shutter was designed and used for all other experiments. This translucent shutter resulted in only a minimal luminance transient when opened. Several control experiments were designed to look at the contribution from masking to the results of the reported experiments.

Three types of controls were completed. One involved repeating the FS experiment with the opaque flag shutter and the translucent shutter, except instead of orthogonal gratings that result in binocular rivalry, same orientation gratings were used that result in fusion under normal viewing conditions. Any suppression at delays around zero msec could represent early luminance masking. On the other

hand, if same orientation gratings do not produce suppression at delays around 500 msec, this would support the view that the suppression demonstrated during FS is due to rivalry not masking.

In another control experiment, we used the translucent shutter, but the view of the left grating was occluded with a diffusing filter. When the shutter was opened, instead of flashing a grating, the left eye was exposed only to the luminance transient normally present in FS and FPS.

The third type of control involved repeating FPS experiments using an oscilloscope image of the grating produced by an image synthesizer. The synthesized grating was flashed with no mean luminance change; therefore, any suppression seen at delays around zero msec could not be due to a luminance transient but might still be due to a type of pattern masking (Schiller, 1965). In addition to FPS, a study was completed where the grating was flashed for only 100 msec and the test probe for 100 msec. These conditions are more like traditional masking experiments (Turvey, 1973), and the results are compared to FPS using the oscilloscope where the grating was flashed for two seconds as usual.

Results

Overall, the results of the masking studies show there is only a small effect from luminance or pattern masking at delays around zero (simultaneous onset of grating and test probe). The suppression seen at longer delays (longer times after onset of suppression) must be due to a rivalry-like suppression and not masking. Additionally, three subjects did a FPS experiment using the 613 nm probe with the left and right eyes on different days. The suppression curves for each eye overlap throughout the entire range of delays indicating that eye dominance was not responsible for suppression seen in these subjects.

Opaque Shutter

Suppression was measured under conditions identical to Experiment 1 except that both gratings were oriented at 45 degrees. Results from three subjects (BB,ML,SB) who all completed Experiment 1 and this control experiment, are presented in Figure 19. Comparison of FS and same orientation data shows that early suppression (delay of 50 msec) of the red and luminance probe might be due in part to luminance masking caused by the opaque shutter. The blue probe seems unaffected by masking at 50 msec, and all probes show minimal suppression at longer delays. The fact that

Figure 19. Same orientation control, opaque shutter. Average of three subjects who completed both Experiment 1 and this control experiment (BB,ML,SB). Conditions were the same as Experiment 1 (FS) except that both gratings were oriented in the same direction . Some early suppression is evident at delay of 50 msec for the red and luminance probes indicating some effect from luminance masking.

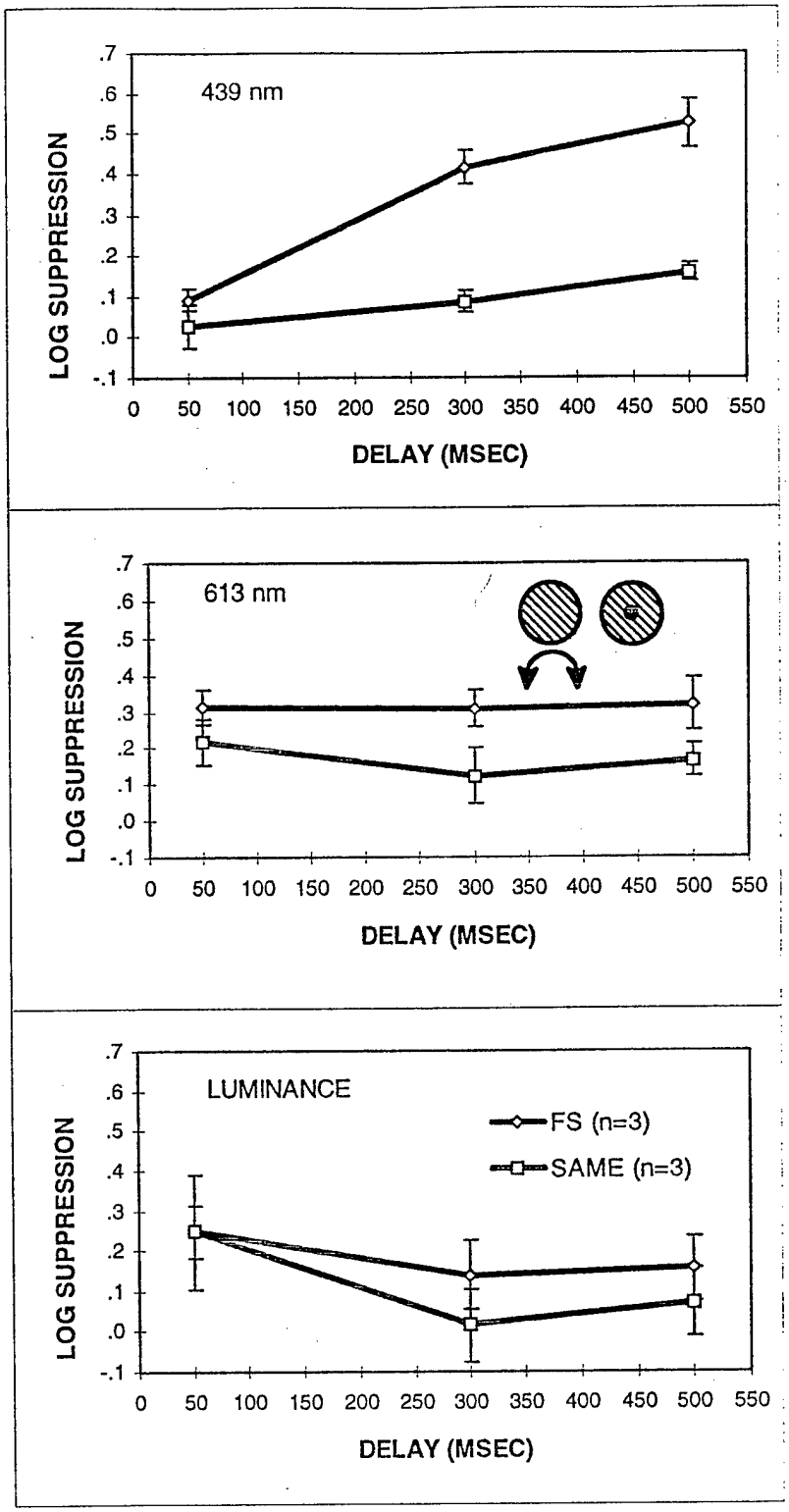
439 nm
LOG SUPPRESSION
.7
.6
.5
.4
.3
.2
.1
.0
-.1
0 50 100 150 200 250 300 350 400 450 500 550
DELAY (MSEC)
613 nm
LOG SUPPRESSION
DELAY (MSEC)
LUMINANCE
FS (n=3)
SAME (n=3)
LOG SUPPRESSION
DELAY (MSEC)

Figure 19.

there is any suppression may be due to a period of right eye suppression which is perceptually undetectable but can be measured with the probe technique.

Translucent Shutter

In Experiments 1 - 4, the luminance of the right grating or homogeneous field was 12 cd/m^2. The light diffusing characteristics of the translucent shutter were such that the luminance of the shutter was close to but slightly less than the luminance seen by the right eye. Since the grating was physically printed and mounted on a rear projection screen, the mean luminance of the grating was 0.18 log units lower than the surround. Therefore, during FS and FPS, when the shutter was opened, there was an unavoidable change in luminance to the left eye not exceeding 0.18 log units. The following experiments show these factors to have a minimal effect on the results reported in Experiments 1 - 4.

A diffusing filter was placed over the left viewing aperture of the apparatus (Figure 7). This filter presented the left eye with a homogeneous field free of any spatial detail; however, when the shutter was opened the left eye saw the same 0.18 log luminance transient as was present in other experiments. The luminance of the right side was made

equal to the left with a neutral density filter and the background illumination adjusted to 12 cd/m^2. A FS type experiment was run with the usual translucent shutter. It is apparent from Figure 20a that luminance masking plays a very minor role in the suppression produced during FS and FPS.

Figure 20b shows an additional control where two subjects from Experiment 2 (EK,TT) were tested under FS conditions with the translucent flag. Instead of orthogonal gratings, same orientation gratings were used. There is essentially no suppression from flashing a same orientation grating at any delay tested. Note that in Experiment 2a, subject EK showed a 1.04 log suppression of the blue probe.

Oscilloscope Generated Grating

As a final series of controls for masking effects, an oscilloscope monitor (Tektronix 608) replaced the rear projection screen as the source of the suppression patterns and background by use of a beam splitter. A 2.6 cpd square wave grating the same size as the earlier FPS experiments was generated with a Picasso image synthesizer. The background was created by the monitor, and the mean luminance of the screen (5 cd/m^2) was lower than other FPS experiments (12 cd/m^2) in order to enhance the contrast of

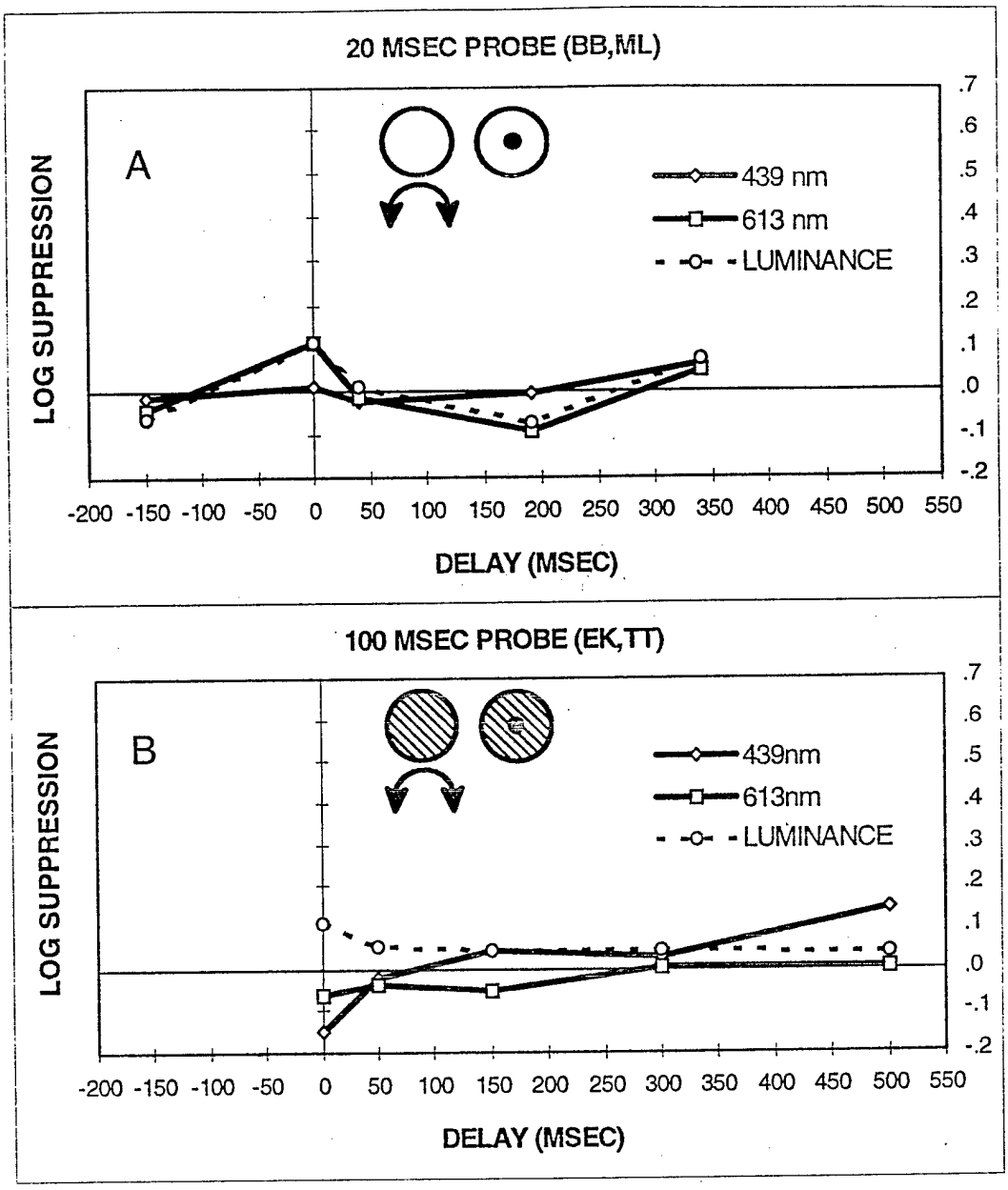

Figure 20. Masking controls. A. Average of BB, ML. Subjects viewed a homogeneous field with the right eye, and a full field, 0.18 log increase in luminance was flashed to the left eye for two seconds. B. Average of EK, TT. Subjects viewed a 2.6 cpd grating with the right eye, and a same orientation grating was flashed to the left eye for two seconds. All other conditions were as in Experiment 2a (Figure 11).

the grating (60%). Instead of the flag shutter, the left grating was presented by the Picasso and therefore was presented to the left eye with no change in mean luminance of the screen. Any early suppression would not be due to luminance masking because no change in mean luminance accompanies flashing of the grating.

FPS vs FPS With Monitor

Flash permanent suppression curves were generated for two subjects (BB,ML) using the monitor grating. Color thresholds were recorded for the blue and red probes as before. Detection thresholds were taken for the luminance probe. The luminance probe was originally designed for detection of a 540 nm increment on a 540 nm background (Schwartz and Loop, 1982). The monitor emits a broad spectral band that peaks at 535 nm. The narrow bandpass of the 540 nm probe peaks near and is contained within the spectral emission of the monitor's P31 phosphor. The 540 nm probe seems to function well as a true luminance probe. Subjects had no difficulty setting blue and red color thresholds on the background created by the monitor.

A comparison of FPS with the translucent shutter and FPS with the monitor is shown in Figure 21. The suppression curves for the blue, red, and luminance probes are quite

Figure 21. Flash permanent suppression masking controls. Average of two subjects (BB,ML) in a FPS paradigm with 100 msec blue (439 nm), red (613 nm), or luminance (540 nm/540 nm bkg) probes. Subjects viewed a homogeneous field with the right eye, and a probe was delivered before or after flashing a 2.6 cpd grating to the left eye. Bold curves compare results of Experiment 2b using the opaque shutter with results using an oscilloscope monitor to generate the grating. Dashed curves("mask") are results of additional controls where the probe duration was 100 msec and the grating was flashed on the monitor for only 100 msec instead of the usual 2 seconds.

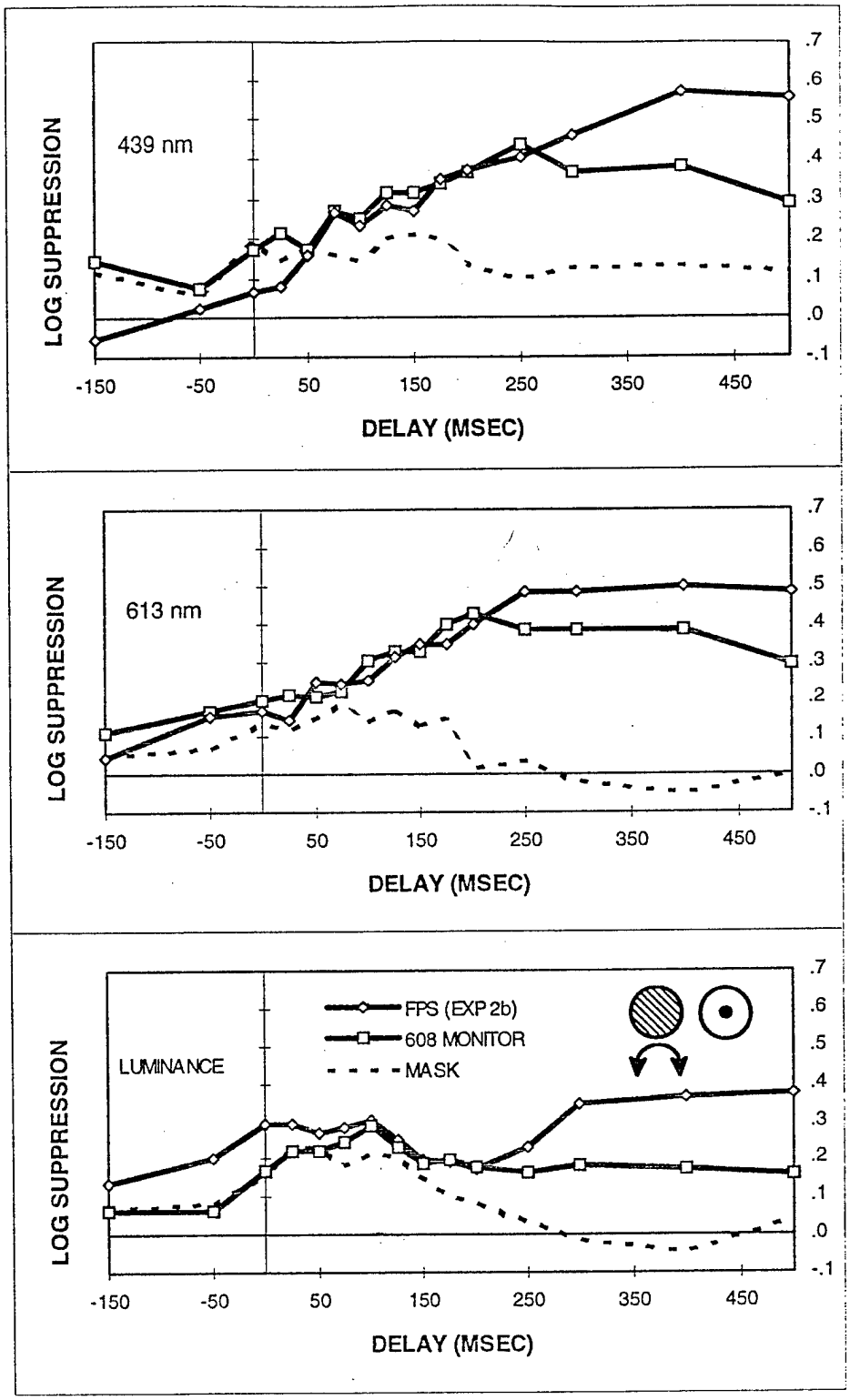
439 nm
LOG SUPPRESSION
.7
.6
.5
.4
.3
.2
.1
.0
-.1
-150
-50
50
150
250
350
450
DELAY (MSEC)
613 nm
LOG SUPPRESSION
DELAY (MSEC)
LUMINANCE
FPS (EXP 2b)
608 MONITOR
MASK
LOG SUPPRESSION
DELAY (MSEC)

Figure 21.

similar except at the longest delays. Since there is no change in luminance when flashing the monitor grating, the rise time in suppression of the probes is not due to the design of the flag shutter.

The magnitude of suppression of the probes at delays of 400 and 500 msec is less with the experiment using the monitor. This difference is probably due to the lower background luminance (5 cd/m^2 versus 12 cd/m^2) and lower contrast (60% vs 80%) of the monitor grating. It has been shown that contrast can effect the magnitude of permanent suppression (Fox, Mauk, and Francis, 1983). At a delay of 500 msec, the subject is essentially viewing a permanent suppression display. Magnitude of suppression during PS was determined for subjects BB and ML with conditions the same as in Figure 21. With the monitor, PS was less than with the high contrast gratings by 0.25 log units (blue), 0.10 (red), and 0.08 (luminance). These differences account for most of the differences in the curves of Figure 23 at the longer delays.

FPS vs MASK

The final masking control used conditions more like conventional dichoptic masking studies (Turvey, 1973). One hundred msec probes seen by the right eye were masked by a

grating flashed to the left eye for 100 msec. In FPS experiments of this work, the grating is flashed for 2 seconds. The results are plotted in Figure 21 as a dashed curve. Masking by the flashed grating is essentially complete by 200 msec. This indicates that transient masking effects from the flashed grating are not responsible for the steady rise in suppression of the probes seen in Experiments 1 through 4.

EXPERIMENT 6: SUPPRESSION OF SUPRATHRESHOLD STIMULUS PROBES

Rationale

For the preceding experiments, magnitude of suppression was determined by increasing the intensity of a probe until it could just be detected, i.e., threshold detection. It is clear that the visual system is suppressed by only about 0.5 log units when tested in this manner. As reviewed by Fox (1991), many interocular suppression studies have involved measuring the detectability of some stimulus change presented during dominance or suppression. For forced choice experiments that generate frequency of seeing curves, these changes must be small because as soon as the strength of the stimulus is even incrementally above threshold, detectability becomes 100% for all trials. If there was any suppression of bright stimuli, it would not be measurable with frequency of seeing curves because the stimulus would be detected 100% for both dominance and suppression.

A high contrast grating, like the 2.6 cpd grating used in our experiments, is itself many orders of magnitude above threshold for its detection. Yet during BR and FS this high

contrast grating is visually suppressed. These observations imply that the suppression mechanism is working on two levels: a very high contrast suprathreshold figure can be easily suppressed, but once suppressed the visual system is "reset" to some new baseline level of sensitivity that takes only 0.5 log units of stimulus strength to "break through" the suppression.

Once a stimulus probe is intense enough to break through suppression, further increases in the intensity of the probe seem not to be suppressed at all because they are always seen. One method to test whether or not there is any suppression to a suprathreshold stimulus is to measure reaction times (RT) to the stimulus. Three results of such a study are possible. RTs could be the same during dominance and suppression if specific visual pathways are unaffected. In fact, RTs have been found to be unaffected by suppression from masking (Fehrer and Raab, 1962). RTs could be longer during suppression for probes at near threshold intensities and quickly shorten to match RTs under dominance when probe intensity increases to a 100% detectable level (for our subjects a .2 - .25 log unit increase). A third possibility is that during interocular suppression, like FS or FPS, there is a level of suppression

(a blockade of visual information) that remains for all stimuli of all intensities. Results of this experiment show that for two of the three subjects, RTs during suppression are longer than during dominance for all probe intensities.

Detailed Procedures

As described in Methods, subjects viewed stimulus probes in dominance and suppression (FPS or FS). Probe presentation was programmed with an electronic clock connected to a response button. RTs were recorded for a range of stimulus intensities for the 1.2 degree, 100 msec, 439 nm probes. Intensities were presented in blocks arranged in a haphazard order where the subject was not aware of the intensity. Probes were presented with an a priori probability of 50% in order to control for anticipation. Only correct responses were recorded. Subjects were able to perform this task easily for intensities at and above threshold. Some dimmer than threshold intensities were attempted but few RTs were recorded, so only intensities at and above threshold are presented below. Reaction times at each intensity are the average of between 20 and 28 RTs; all of the brighter points have at least 25.

Results

Figure 22a shows results for subject BB during FPS at a delay of 500 msec (500 msec into the suppression process). These intensities span a 2.5 log range, and suppression is maintained at all intensities. The brightest intensity (0.4) was collected in a separate experiment and merged with the data. The RTs at this intensity were dominance 228 msec +/- 19 (sd), and suppression 244 msec +/- 16. This difference was significant (two tailed t-test, $p<.001$).

Figure 22b shows FPS results for KW and ML. KW had RTs that were equivalent at intensities greater than about 0.5 log units above threshold. ML appears to show residual suppression for intensities over a 1.5 log unit range.

Subjects BB and ML had about 0.5 log units of suppression measured by method of adjustment during the experiment whereas KW only had 0.2. Perhaps his overall lower amount of suppression to this type of display is partly responsible for the merging of RTs at higher intensities for KW.

Figure 23 shows results of the same type of procedure except when two orthogonal gratings were used (flash suppression). It is clear that some suppression remains for suprathreshold stimulus probes under these conditions.

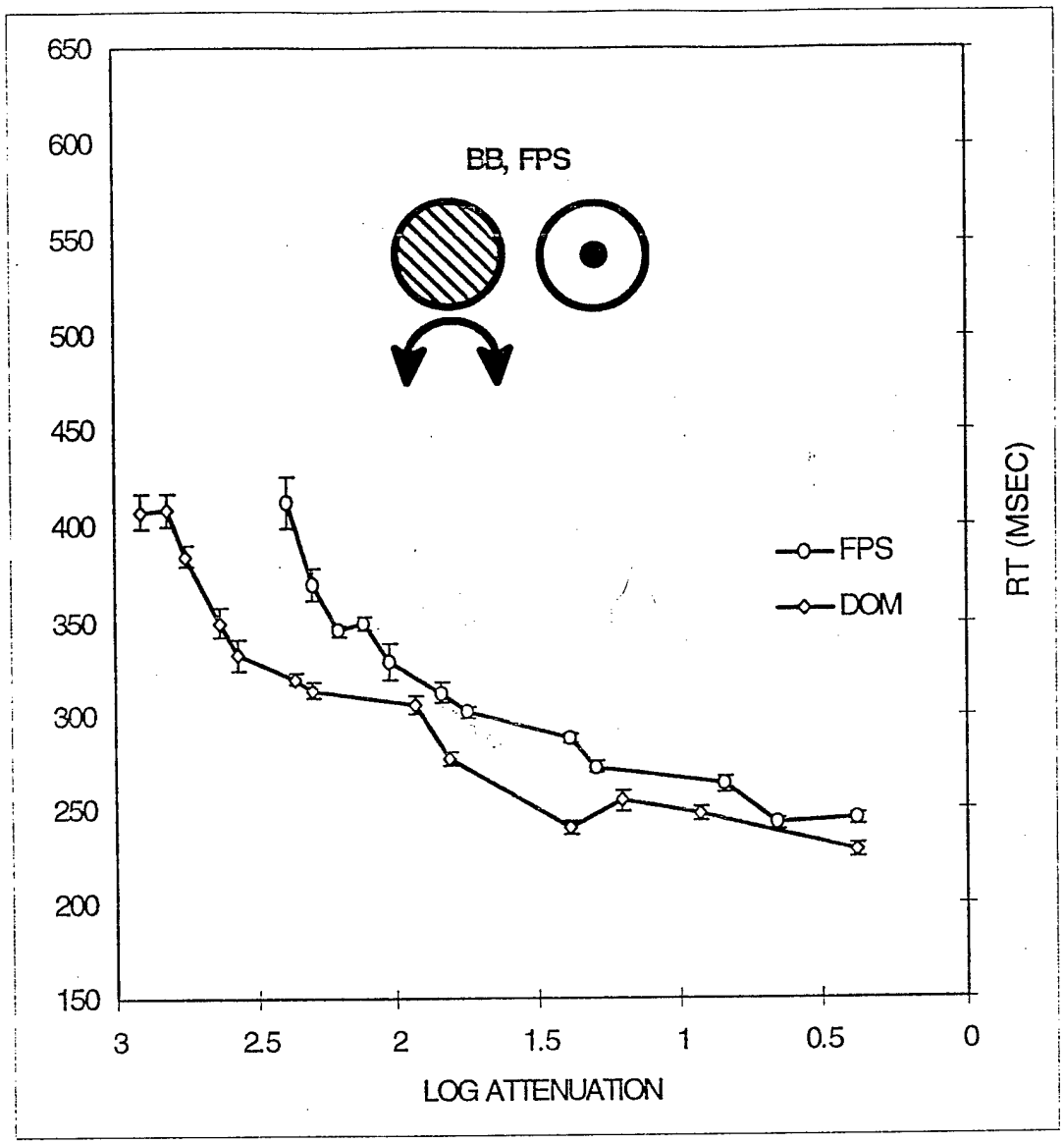

Figure 22a. Suppression of suprathreshold stimulus probes, flash permanent suppression. Subject BB recorded reaction times to stimulus probes for a range of intensities in dominance and suppression. The uppermost point on each curve represents thresholds determined by method of adjustment during FPS. The abscissa represents attenuation of the probe by the ND wedge. Smaller numbers indicate brighter probes. Note that suppression is maintained for all probe intensities. Error bars represent +/- one SEM.

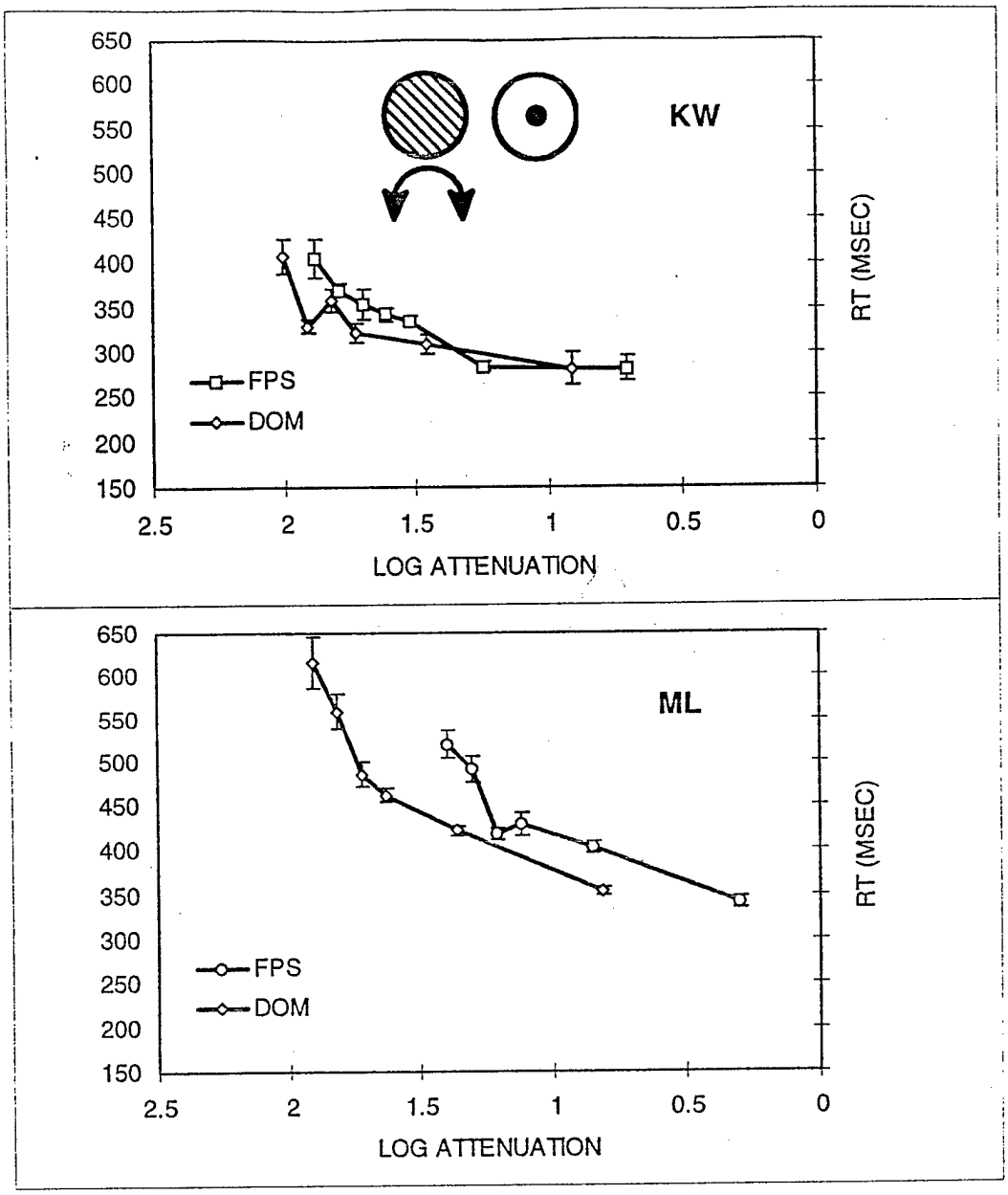

Figure 22b. Suppression of suprathreshold stimulus probes, flash permanent suppression. Subjects KW and ML recorded reaction times to stimulus probes for a range of intensities in dominance and suppression. The uppermost point on each curve represents thresholds determined by method of adjustment during FPS. Error bars represent +/- one SEM.

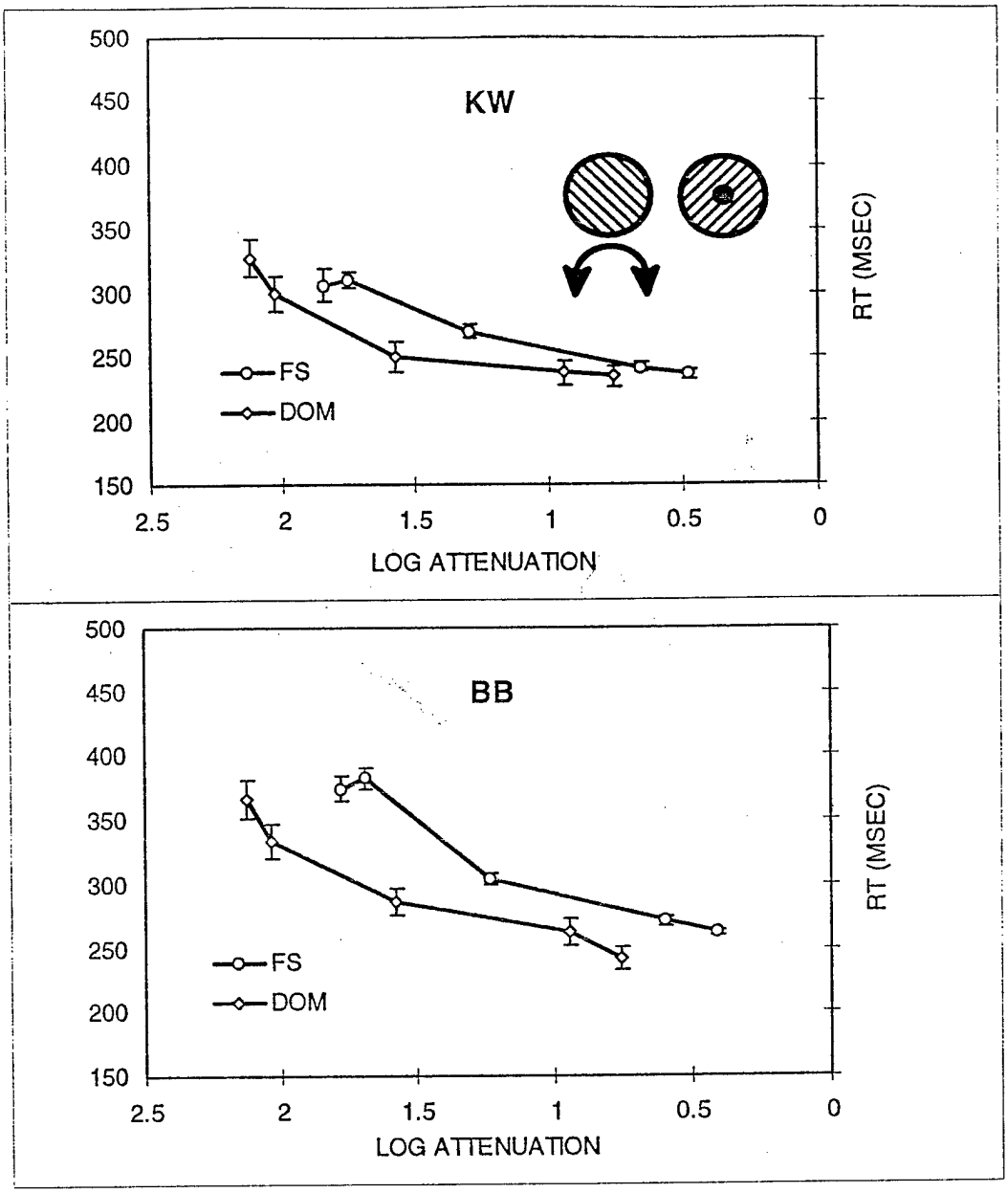

Figure 23. Suppression of suprathreshold stimulus probes, flash suppression. Subjects KW and BB recorded reaction times to stimulus probes for a range of intensities in dominance and suppression. The uppermost point on each curve represents thresholds determined by method of adjustment during FS. The abscissa represents attenuation of the probe by the ND wedge. Smaller numbers indicate brighter probes. Error bars represent +/- one SEM.

DISCUSSION

Results of these studies are important to theoretical concepts of interocular suppression and to practical clinical aspects of suppression like designing new amblyopia therapies. First some implications of these studies to neural theory and the relationship between the results and recent studies from other laboratories will be presented. Neural theory should be and is intimately related to discussions of amblyopia therapy that follow.

Theoretical Implications

The often discussed dichotomy within the visual system consisting of a partitioning of neural anatomy and physiology into transient versuss sustained subsystems (Breitmeyer and Ganz, 1976), or magnocellular versus parvocellular subsystems (Livingstone and Hubel, 1987) forms a basis for theories of perception. Although there is considerable overlap between subsystems, it is generally agreed that they operate in parallel to form the opponent-color and broad band (luminance) channels in the primate, and presumably human, visual system (Schiller, Logothetis

and Eliot, 1990). As shown by King-Smith and Carden (1976), processing by the opponent-color and luminance subsystems can be probed and identified psychophysically. Our flash suppression and flash permanent suppression results offer psychophysical insight into the temporal profile of suppression interactions within the opponent-color and luminance systems (Experiment 3).

Figures 11, 13, and 15 show that the opponent-color system is suppressed with a different time course than the luminance system. If these qualities could be identified in a neural substrate, then contributions to suppression from the opponent-color and luminance systems could be identified in higher cortical areas. For example, a visual neuron can be identified in the visual system that responds to either colored or achromatic stimuli. In a FPS paradigm, the neuron might take on a suppression time course like that of our stimulus probes. This would be one way of linking a perception with a physiology.

Recent experimental results may necessitate a complete re-thinking of the neural basis for binocular rivalry suppression. Logothetis, Leopold, and Sheinberg (1996) have shown that rivalry from orthogonal gratings may not be caused by competition from right and left monocular channels

as is posited by all models of BR (Blake, 1989; Lekhy, 1988; Lehky and Blake, 1991; Wolfe, 1986). Instead, Logothetis et al. have shown that normal appearing BR can be produced by rapidly flickering and alternating orthogonal grating stimuli to each eye. The resulting BR alternations do not correlate with the flicker because the rate of flicker is much faster than the BR alternation rate. The distribution of dominance durations from the flicker induced rivalry can be fit to a gamma distribution (Fox and Herrmann, 1967) just like normal BR. Logothetis et al. suggest that the perception of rivalry originates at a higher cortical level than striate cortex and is not competition between monocular inputs but is more like a multistable phenomenon seen with ambiguous figures, such as the Schroeders staircase illusion or Necker cube.

Their conclusions should be evaluated with some caution. We know that length of time that flashed orthogonal gratings are viewed determines if there is fusion or rivalry (Wolfe, 1983). Alternately flickering rivalry gratings to subjects might just cause some interaction of temporal summation and grating adaptation that leads to the BR-like perceptual alternations. Personal observations have shown that flashing a left grating on and off for 100 msec

while viewing a grating with the other eye also leads to BR-like alternations with a rate much like normal BR.

Perhaps a better way to probe higher visual centers for interocular suppression might be in a FPS paradigm where some neural correlates of suppression must be present at some level and might be found. Inferior temporal cortex neurons of alert monkeys are markedly suppressed under masking conditions (Tovee, Rolls, Treves, and Bellis, 1993). Suppression of the neural response was tightly linked to the masking stimulus and correlated exactly with perceptions described by human observers viewing the same display. Flash suppression techniques have been used recently to explore the visual cortex for a suppression response (Scheinberg, Leopold and Logothetis, 1996; Sengpiel, Blakemore and Harrad, 1995). These techniques could be extended and used to probe many areas of the brain. A knowledge base of human observations related to FS is needed in order to draw conclusions and comparisons between human and neurophysiological data.

One mystery of the binocular rivalry process is how one high contrast grating can disappear from perception while a stimulus probe less than two times threshold can "break through" the suppression. For example, blue, red, and

luminance probes just 0.5, 0.25, or 0.1 log units above threshold can be detected during the suppression phase of BR, FS, or PS. A possible insight into this mystery may have come from recent neurophysiological studies of alert monkeys viewing BR stimuli. Leopold and Logothetis (1996) found that about one third of the visual cortex neurons studied decreased their firing rate as the monkeys reported suppression of a BR stimulus. However, more than two thirds of the total population of cells continued to respond when the monkeys reported suppression. These results suggest that there is not a total blockade of one eye's information during BR. The observation that a considerable amount of visual input into the suppressed eye remains is consistent with the fact that only a small, 0.5 log unit increase in stimulus strength is necessary to overcome suppression.

Perception of one image or the other during BR may be selected by processing of the total population of active and inactive neurons in many parts of the brain as suggested by Leopold and Logothetis (1996). It may be possible to identify specific neurons and neural connections related to the perception or suppression of an image. FS techniques would allow a fast method of identifying broadband or color

coded cells and relate their connections to the physiology of suppression

FS, FPS, and PS can be used to explore the site of interocular suppression in general and to specifically probe sensitivities of the opponent-color and luminance systems. On a more practical level, these techniques can be used to investigate the nature of clinical suppression and perhaps lead to better treatment methods.

Clinical Suppression and Amblyopia Therapy

Is the suppression seen during PS, BR, FPS, and FS the same as suppression seen during strabismus or amplyopia? Spectral sensitivity functions of strabismics do not show the wavelength specific loss of sensitivity seen in normals during BR (Smith, Levi, Manny, Harwerth, and White, 1985), which suggests that suppression mechanisms are different. Others have argued that the same suppression mechanisms are operative in BR and strabismus (Fahle, 1983; Sengpiel et al., 1994). Perhaps young strabismic or amblyopic subjects would show suppression patterns like those in BR or PS if tested under the proper conditions. There are a number of similarities between findings in abnormal binocular vision and the results of Experiments 1 - 6.

Harwerth and Levi (1978) performed a number of tests on normal and abnormal subjects. They found in amblyopes that the opponent-color system is suppressed more than the luminance system. There was not, however, a selective loss of sensitivity for the short wavelengths as seen in normals during BR and FS.

They also found that temporal summation was reduced for the amblyopic eye. Their Figure 6 shows that for a 5.0 cpd grating contrast sensitivity in the amblyopic eye improves at a slower rate with increases in the duration of the stimulus than the normal eye. If magnitude of suppression from amblyopia is calculated from their Figure 6, a greater suppression would be evident for longer duration stimuli. These findings are in agreement with results from Experiment 4 where longer duration probes are suppressed more, apparently due to reduced temporal summation during FPS.

Harwerth and Levi also measured reaction times to various levels of contrast for gratings of various spatial frequencies. For all spatial frequencies, but especially higher spatial frequencies, RTs in the amblyopic eyes remained prolonged over a 1.5 log increase in contrast. RTs during FPS in normal observers are also prolonged (Experiment 6, Figures 22a,b). Harwerth and Levi concluded

that sustained channels are selectively impaired over transient channels in amblyopia and suggest that amblyopia treatment might focus on this difference.

We know that manipulating interocular differences in the visual input of amblyopic subjects can result in improvement in visual function of the amblyopic eye. Normally, when both eyes are opened, an amblyopic eye is suppressed. Placing neutral density filters over the good eye can restore some function of the amblyopic eye (Leonards and Sireteanu, 1993). Improvement in vision of an amblyopic eye under binocular conditions is also possible by alternately flickering visual input to each eye (Schor, Terrell, and Peterson, 1976). The improvement in acuity is dependent on the duration of the "flashed" stimulus, with greater improvements seen with durations of 75 and 250 msecs. Technology is available to provide long term, computer programmed, alternating stimuli to the two eyes. Logothetis, Leopold, and Shienberg (1990) used liquid crystal shutter (LCS) goggles to alternate the visual input to their subjects as a way to induce rivalry. Commercially available LCS glasses are used for stereopsis testing (Rutstein, Fuhr, and Schaafsma, 1994), and could be modified

to present precise timing of visual input to an amblyope undergoing therapy.

To know what type of input to program into a display using LCS glasses and perhaps a computer screen, more information is needed about the visual function of amblyopes. In particular, the time course and magnitude of suppression during FS and FPS would offer insight into the temporal properties of suppression in these subjects. Also the patterns of suppression with respect to the color and luminance systems as well as sensitivity to other types of visual stimuli would be needed in order to design a visual display used to overcome suppression. To date there is little treatment available for amblyopia other than patching the good eye or viewing some orthoptic computer displays. Although there is a critical period for overcoming permanent vision loss from strabismus, amblyopia or both (Hubel and Wiesel, 1965), improvements in visual function are often seen in older subjects (Rutstein and Fuhr, 1992; Wick, Wingard, Cotter, and Scheiman, 1992). Further investigations into the nature of suppression in subjects with normal and abnormal binocular vision are needed to identify and treat problems caused by visual suppression.

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